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ON THE STRUCTURE OF THE SNOUT OF CROSSOPTERYGIANS AND LOWER GNATHOSTOMES IN GENERAL

BY

ERIK JARVIK

With 87 figures in the text and 17 plates

UPPSALA 1942
ALMQVIST & WIKSELLS BOKTRYCKERI-A.-B.

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ON THE STRUCTURE OF THE SNOUT OF CROSSOPTERYGIANS AND LOWER GNATHOSTOMES IN GENERAL

INAUGURAL DISSERTATION

BY

ERIK JARVIK

FIL. LIC., VÄSTG.

WITH 87 FIGURES IN THE TEXT AND 17 PLATES

BY DUE PERMISSION OF THE PHILOSOPHICAL FACULTY OF THE UNIVERSITY OF UPPSALA, TO BE PUBLICLY DISCUSSED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY, IN THE LECTURE-ROOM OF THE PALAEONTOLOGICAL INSTITUTE, ON SATURDAY, DECEMBER 12TH, 1942, AT 10 A. M.

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On the Structure of the Snout of Crossopterygians and Lower Gnathostomes in General.

By

ERIK JARVIK
(Stockholm).

With 87 figures in the text and 17 plates.

Contents.

Page
Preface 237
I. Introduction 240
II. Terminology 241
III. Review of the snout in certain recent forms 250
  A. Elasmobranchs, with special reference to Chlamydoselachus . 250
  B. Brachiopterygii (Polypterus) 256
  C. Sturgeons, Amia, and other Actinopterygians 265
  D. Dipnoi 270
  E. Urodela, with special reference to Salamandra 284
  F. Anura, with special reference to Rana 308
IV. The snout in Crossopterygians 334
  A. Sensory canals and dermal bones 334
  B. The snout in Porolepiformes 353
    1. Descriptive section 353
      a. Porolepis 353
      b. Holoptychius 379
    2. Comparative section 382
      a. Comparison with Selachians and other Elasmobranchs . 382
      b. Comparison with Brachiopterygii (Polypterus) 390
      c. Comparison with Actinopterygii 390
      d. Comparison with Dipnoi 391
      e. Comparison with Urodela 392
      f. Comparison with Anura 424
  C. The snout in Osteolepiformes 425
    1. Descriptive section 425
      a. Eusthenopteron foordi 425
      b. Remarks on other Osteolepiformes 481

Page
2. Comparative section 488
   a. Comparison with Porolepiformes 488
   b. Comparison with other fishes 495
   c. Comparison with Urodela 495
   d. Comparison with Anura 495
D. The snout in Coelacanthiformes 554
1. Descriptive section 554
   a. Euporosteus, Nesides, and Diplocercides 554
   b. Dictyonosteus 579
   c. Remarks on Postdevonian fossil Coelacanthids 582
   d. Remarks on Latimeria 585
   e. General remarks 592
2. Comparative section 593
   a. Comparison with Porolepiformes and Osteolepiformes . 593
   b. Comparison with Elasmobranchs 597
   c. Comparison with Brachiopterygii (Polypterus) 598
   d. Comparison with Actinopterygians 612
   e. Comparison with Dipnoi 620
   f. Comparison with Urodela and Anura 621
V. Remarks on the snout in Stegocephalians 621
VI. Conclusions and summary 641
VII. Bibliography 652

Preface.

In 1935 I commenced a study of the dermal skeleton of the Crossopterygian fish *Eusthenopteron foordi* Whiteaves. The investigation was based on a comprehensive material belonging to the Palaeozoological Department of the Swedish Museum of Natural History (Riksmuseum) in Stockholm, the Palaeontological Institute of the University of Uppsala, the British Museum of Natural History in London, the Royal Scottish Museum in Edinburgh, the Sedgwick Geological Museum, Cambridge, and the Dartmouth College, Hanover, N. H., U. S. A. This material enabled me to examine not only the general arrangement of the dermal bones and the sensory canals, but also their development in detail.

When studying the *Eusthenopteron* material just mentioned and upon examining a comprehensive material of other Crossopterygians which I had for purposes of comparison, I found, however, that the structure of the snout of the Crossopterygians, the knowledge of which has hitherto been most incomplete, was highly interesting from an anatomical point of view. I decided therefore to postpone the publication of the monograph on the dermal skeleton of *Eusthenopteron* originally planned and to give instead a description of the structure of the snout of Crossopterygians in general. My first intention was then to deal with both the endocranium and the dermal bones in detail. In view of the fact that a complete description of the dermal bones of the snout necessitates a great number of plates and owing to the difficulty of having printed under the present circumstances a treatise of the size required in dealing fully with the snout of the Crossopterygians, I have had to confine this paper to the endoskeleton of the snout. The dermal bones are dealt with only when the knowledge of these is of particular importance for the understanding of the anatomy of the snout.

In addition to the above-mentioned material of *Eusthenopteron foordi* I have had at my disposal the following material of fossil Crossopterygians: 1) Two grinding series through skulls of *Eusthenopteron foordi.* 2) The material of *Eusthenopteron wenjukowi* (Rohon) and *E. säve-söderberghi* Jarvik previously described by me (1937), and fresh material of *E. säve-söderberghi*, comprising inter alia the tip of the snout of the holotype of this species. 3) Comprehensive material of *Porolepis* Woodward from the Lower Devonian of Spitzbergen. 4) A likewise comprehensive material of *Holoptychius* from the uppermost Upper Devonian of East Greenland. 5) Some specimens of Osteolepids and Holoptychids from the Old Red Sandstone in England and Scotland. These specimens, several of which were returned before the outbreak of war, had been borrowed by Professor G. Säve-Söderbergh of Uppsala from various English and Scottish museums. 6) A grinding-series through the skull of the Devonian Coelacanthid *Nesides schmidti* Stensiö. 7) The other material of Devonian Coelacanthids (*Euporosteus eifelianus* Jaekel, *Diplocercides kayseri* (v. Koenen), *Nesides schmidti* Stensiö) so far known. 8) The holotype of *Dictyonosteus arcticus* Stensiö, and 9) for a short time the undetermined Coelacanthid from the Triassic of East Greenland preliminarily described by Nielsen in 1936 (pp. 15—19; figs. 8—10, 14—16).

Recent material has to some extent been studied for comparison. Heads of *Polypterus bichir*, *P. senegalus*, *Acipenser sturio*, *Rana esculenta* and *Bufo marinus* have been dissected and reproduced in this work. The anterior part of the endocranium of an *Acipenser*-specimen dealt with by Professor Stensiö in 1932 (figs. 34, 35) has also been figured here.

On the basis of the above-mentioned fossil material a detailed description of the structure of the snout of *Porolepis*, *Eusthenopteron*, *Euporosteus*, and *Nesides* could be given. It could also be established that with regard to the structure of the snout the Crossopterygian forms known to us at present (cf. Woodward 1932, pp. 109—115) include three widely different groups, viz.

1) *Porolepiformes*, comprising *Porolepis* and Holoptychids.
2) *Osteolepiformes*, comprising Osteolepids and Rhizodontids.
3) *Coelacanthiformes*, comprising Coelacanthids and *Dictyonosteus*.

By detailed comparisons with recent lower Gnathostomes I have been able to reconstruct with comparatively great certainty the course of the blood vessels and nerves in the snout of the fossil Crossopterygians examined and to add in many other ways to our knowledge of the soft parts of the snout of the Crossopterygians. The thorough knowledge of the structure of the snout of various Crossopterygians acquired through studies of the fossil material and through comparisons with recent forms has enabled me to discuss the affinity of the various groups of Crossopterygians with other lower Gnathostomes and to contribute to the question of the phylogeny of the Amphibians.

For loans of material I am indebted in the first place to the following gentlemen: Dr. C. Forster-Cooper, London; Dr. W. Graham-Smith, Cambridge; Dr. W. Gross, Berlin; Professor A. Heintz, Oslo; Dr. W. Janensch, Berlin; Dr. Lauge Koch, Copenhagen; Dr. E. Nielsen, Copenhagen; Dr. F. R. PARRINGTON, Cambridge; Professor B. M. PATTEN, Cleveland, Ohio, U. S. A.; Dr. G. M. ROBERTSON, Dartmouth College, Hanover, N. H., U. S. A.; Professor R. SPÄRCK, Copenhagen; Dr. A. C. STEPHEN, Edinburgh; Professor G. SÄVE-SÖDERBERGH, Uppsala; Dr. E. I. WHITE, London. I owe my thanks to Professor H. RENDAHL, Stockholm, for some specimens of recent *Anura*.

For the preparation of plates and text-figures grants have been received from Regnells Zoologiska Gåvomedel, Bibliotekarien Johan August Ahlstrands Donation, and Längmanska Kulturfonden. For the Letterstedt Award (Letterstedtska understödet för särskilt maktpåliggande undersökningar) I beg to express my thanks to the Royal Academy of Science of Stockholm.

The present paper has been elaborated in the Palaeozoological Department of the Swedish Museum of Natural History (Naturhistoriska Riksmuseet) in Stockholm.

The preparation of the specimens was carried out partly by the author, but mainly by Miss A. BRASCH. The drawing and retouch work was done by Mr. S. EKBLOM. In the photographic work I was assisted by Mr. G. AHL. The necessary stylistic corrections of the manuscript were made by Mr. B. NORBELIE. To all these collaborators I wish to express my sincere thanks.

I. Introduction.

The term snout as used in this work refers to the anterior part of the head in which are situated the olfactory organs, the nasal tubes, and the nostrils. In certain forms the posterior nostrils and the posterior openings of the ductus nasolacrimalis lie much behind the olfactory organ, even so far backwards as beneath the middle part of the orbital opening. The term snout, as defined here, therefore includes the whole anterior part of the head from the tip of the snout backwards to about the middle of the orbital openings, though excluding the lower jaw apparatus, or, more precisely: 1) the entire ethmoidal region of the neural endocranium, the part of the orbitotemporal region of the neural endocranium situated in front of the opticus canals, and the dermal bones developed on these two parts of the endocranium; 2) the anterior part of the palatoquadrate-cheek complex (the anterior part of the palatoquadrate and its dermal bones and the anterior part of the dermal bones of the cheek); and, finally 3) the soft tissues connected with all the skeletal parts and elements mentioned (the anterior part of the brain, the nasal sacs, the olfactory nerves and other nerves, the arteries and veins, the oblique muscles of the eyes, the nasal glands, etc.).

I have treated the ethmoidal region most comprehensively, describing it in detail in a number of forms. A detailed description has also been given of the anterior part of the palatoquadrate (pars autopalatina palatoquadrati) and its articulations with the neural endocranium. On the other hand, the orbitotemporal region of the endocranium has been treated more summarily, particularly as regards exterior characteristics. The dermal bones have been treated where they are developed in relation to the nasal tubes or for other reasons. However, a summary of the general arrangement of the dermal bones of the snout in one representative of each of the three main groups of Crossopterygians has been given.

The following classification of the Crossopterygians is used in this work (only such genera as have been dealt with or referred to are mentioned):

Crossopterygii.

I. Rhipidistia.
  A. *Porolepiformes.*
    1. Fam. *Porolepidae: Porolepis.*
    2. Fam. *Holoptychiidae: Holoptychius, Laccognathus, Glyptolepis.*
  B. *Osteolepiformes.*
    1. Fam. *Osteolepidae: Osteolepis, Thursius, Diplopterax, Ectosteorhachis* (*Megalichthys*), *Glyptopomus.*
    2. Fam. *Rhizodontidae: Eusthenopteron, Tristichopterus, Sauripterus, Rhizodopsis, Rhizodus, Strepsodus.*

II. Actinistia.
  A. *Coelacanthiformes.*
    1. Fam. *Coelacanthidae: Dictyonosteus, Euporosteus, Nesides, Diplocercides, Rhabdoderma, Coelacanthus, Spermatodus, Wimania, Axelia, Mylacanthus, Scleracanthus, Laugia, Whiteia, Undina, Macropoma, Latimeria.*

To be able to explain the conditions in the fossils it has been necessary to enter to a great extent also upon the anatomy of recent forms. I have found it suitable, therefore, to give a summary of the structure of the snout in the principal groups of the lower Gnathostomes. As a rule only one form in each group has been dealt with in detail. I have not touched upon deviating forms such as the *Holocephali* among the Elasmobranchs, the *Perennibranchiata* among the Urodeles, and the *Aglossa* among the *Anura*. When referring in this paper to Elasmobranchs, Urodeles and *Anura* I thus do not take into account the three groups of forms mentioned.

II. Terminology.

In the present paper the Crossopterygians will be thoroughly compared both with other fishes and with lower Tetrapods. To make this comparison easier to understand a uniform anatomical terminology has been used for all Gnathostome Vertebrates. Such anatomical terms as have been used previously in different senses for fishes and Tetrapods have been rejected and others introduced. For other reasons, too, it has been necessary to abandon old and suggest new anatomical terms. The anatomical terminology employed here is thus to some extent different from that found in earlier anatomical works and text-books (ECKER-WIEDERSHEIM-GAUPP 1896, 1899, 1904; PETER 1901; GAUPP 1905; ALLIS

1922, 1923; GOODRICH 1930; FRANCIS 1934; MATTHES 1934; HOLMGREN and STENSIÖ 1936; STADTMÜLLER 1936; DE BEER 1937).

Before explaining the general terminology employed here I would like to discuss a few old terms which are in some way or other incorrect, misleading or otherwise unsuitable.

"Nasenhöhle" or cavum nasi is used by GAUPP (cf. ECKER-WIEDERSHEIM-GAUPP 1904, pp. 621—679) in two or three different senses. He uses it to denote sometimes the nasal cavity formed by the skeleton itself, sometimes the cavity enclosed by the nasal sac. It is also probable that by these two terms he refers both to the cavity in the skeleton itself and to the nasal sac and its cavity. So vague a terminology naturally tends to create confusion. When discussing both the hard and the soft anatomy of the snout it is necessary to make a sharp distinction between such cavities as are formed by the skeleton and those surrounded by soft parts.

In the literature the expression external nasal openings refers either to the external orifices of the nasal tubes or (particularly in palaeontological literature) to the skeletal foramina for the nasal tubes. These openings in the skeleton and in the soft tissues are, of course, not identical and must be differently termed. As to the openings for the nasal tubes in the skeleton itself we should furthermore distinguish between those of the endoskeleton and those of the exoskeleton.

To denote different parts of the endoskeleton authors often use terms containing the word planum. Such terms, e. g. planum antorbitale, planum terminale, planum conchale, may, however, easily give rise to misunderstanding, as the word planum (latin *planus*, level, flat) may easily convey the idea that a surface is meant (regarding planum triangulare cf. ECKER-WIEDERSHEIM-GAUPP 1904, p. 645 and STADTMÜLLER 1936, p. 553). Words combined with cartilago are frequently employed as names of skeletal elements and skeletal parts built up of cartilage, e. g. cartilago obliqua, cartilago alaris. However, such terms cannot be used for forms in which the endoskeleton is ossified, as is the case with the Devonian Crossopterygians dealt with here. Instead of "planum" and "cartilago", which have been avoided for the reasons mentioned, I have introduced such terms as pars, lamina, processus, etc. (e. g. pars terminalis instead of planum terminale and lamina obliqua instead of cartilago obliqua).

The wall which on each side separates the orbit from the nasal cavity was called by GAUPP (1905, p. 587) Planum antorbitale. This name refers, however, only to the position of the wall in relation to the orbit. Just as it is most natural to commence the description of the endocranium at the foremost part, it is also most natural in a denomination of the various parts of the endocranium to begin with the foremost one. The wall in question should then be named after its position in relation to the nasal cavity. As "planum" should be avoided, the wall will simply be called the postnasal wall.

The postnasal wall of Amphibians has been treated by a number of authors (De Villiers, Ramaswami, Francis, Pusey, and others) under the term of processus (cartilago) antorbitalis. However, in the literature the term processus antorbitalis is met with in at least another two senses. In sharks (Allis 1923, pp. 144—146; Holmgren and Stensiö 1936, p. 310; figs. 238—241; cf. Holmgren 1941, p. 7) it is used for that part of the postnasal wall which in adults lies dorso-medially of the profundus canal, whereas in embryological works (Gaupp 1905; Goodrich 1930, pp. 247, 249; Stadtmüller 1936, p. 546) it is applied to a lateral process from the trabecula, a process which forms certain posterior parts of the nasal capsule, but usually only the ventral or ventro-lateral part of the postnasal wall (in regard to the *Anura* see below, p. 321). This process from the trabecula is called lamina orbitonasalis by De Beer (1937), who however sometimes uses this term (op. cit. p. 395) also for the whole "planum antorbitale", i. e. the entire postnasal wall. As the lamina orbitonasalis forms only a part of the postnasal wall, it is unsuitable as a term synonymous for the postnasal wall. Lamina orbitonasalis should thus be used exclusively in its limited sense as a designation for the embryonic process from the trabecula.

As regards both the foramina and canals through which run vessels and nerves from the orbit to the nasal cavity and the more important foramina through which the profundus branches leave the nasal cavity the terminology used has been both inconsistent and confusing. The opening or canal in the postnasal wall through which the so far essentially unbranching n. profundus from the orbit reaches the nasal cavity was called by Gaupp (1905, pp. 671, 698, 730) Foramen orbitonasale. By De Beer (1937, pp. 55, 92, 388, 395, 432) this opening or canal was called "the orbitonasal foramen", while the very similar term "the orbitonasal canal" (De Beer 1937, pp. 55, 92, 395) is by him used of a vein canal from the orbit to the nasal cavity, a vein canal whose homologues in different groups are anything but clear. In sharks Holmgren and Stensiö (1936, p. 306) use "Orbitonasalkanal" for the canal through the postnasal wall which gives passage to the orbitonasal vein, whereas in *Polypterus* they (Holmgren and Stensiö 1936, fig. 294) refer by the same term to an artery canal running from the orbit to the canalis olfactorius. Since the term "orbitonasal canal" has, consequently, been employed in many differing senses, I have not made use of it here. Those foramina or possibly canals through which the lateral and medial nasal branches of the n. profundus in Tetrapods pass forwards from the nasal cavity are referred to by Gaupp (1905, p. 587) as foramen epiphaniale and foramen apicale respectively. However, De Beer (1937, pp. 68, 82) uses foramen epiphaniale in quite another sense in sharks and *Polypterus*, viz. of an opening in the postero-medial part of the roof of the nasal cavity; this opening lets through the n. profundus which is essentially unbranching even so far forward in these forms. This opening can, of course, not be homologous to the opening for the lateral nasal branch of the n. profundus in Tetrapods, for which Gaupp introduced the name foramen epiphaniale. Foramen apicale has been employed by Stadtmüller, Chung, Francis, and others to denote in *Urodela* any of the many openings in the roof of the nasal cavity and adjoining parts of the anterior and medial walls through which the medial nasal branch of the n. profundus, which is divided into minor branches, leaves the nasal cavity (see below p. 291). It is impossible, however, to accept this use of the term foramen apicale, because no "foramen apicale" exists in Urodeles. The workers mentioned have not realized this fact. In their endeavours to identify the foramen apicale in Urodeles they have simply called one of the many profundus openings foramen apicale with the result that entirely different openings have been thus denoted. Both Gaupp (1905, p. 732; Ecker-Wiedersheim-Gaupp 1896, p. 47), Stadtmüller (1936, p. 556; figs. 412, 414) and others have used in *Anura* the term fenestra nasobasalis instead of foramen apicale.

In higher Tetrapods, e. g. reptiles (Gaupp 1905, fig. 383; De Beer 1937; pl. 83, fig. 3; pl. 93, fig. 4) and mammals (Goodrich 1930, fig. 264; Stadtmüller 1936 a, figs. 641, 656, 662), the fenestra endonarina anterior (fenestra narina of previous authors) lies apically and is separated from the fenestra endochoanalis (fenestra basalis s. choanalis) by a cartilaginous bridge formed in the floor of the nasal cavity. This bridge, which as a rule is narrow and connects the ventral part of the lateral wall of the nasal cavity with the ventral part of the septum nasi, was called lamina transversalis anterior by Gaupp (1905, p. 587; cf. Goodrich 1930, p. 247; De Beer 1937, p. 396). In the majority of Amphibians and, as will be seen later, also in the Rhipidistid Crossopterygians, however, the fenestra endonarina is an opening in the lateral wall of the nasal cavity. In these forms, therefore, the fenestra endonarina is separated from the fenestra endochoanalis by a ventral part of the lateral wall of the nasal cavity (*Anura, Osteolepiformes* among the Rhipidistid Crossopterygians) or by a ventral part of the said wall together with an adjoining lateral part of the floor of the nasal cavity (*Urodela, Porolepiformes* among the Rhipidistid Crossopterygians). It has not been possible for me to consider higher Tetrapods in this work and I cannot, therefore, take up a position towards the question whether the septum separating the fenestra endonarina from the fenestra endochoanalis in lower Tetrapods is homologous to the lamina transversalis anterior. As this septum in many respects differs from the lamina transversalis anterior, I have considered it most suitable to refer to it under the term of lamina nariochoanalis.

In the present paper I have used the following general terminology which is purely descriptive (see fig. 1).

The ethmoidal region (*Eth. reg*) of the endocranium or the ethmoidal region, as it will mostly be called, refers to the foremost part of the endocranium situated anteriorly to a transverse plane through the posterior (orbital) orifice of the canal for the unbranching n. profundus (the majority of fishes) or through the posterior orifice of the canal for the medial nasal branch of the n. profundus (Rhipidistid Crossopterygians, Tetrapods). The ethmoidal region encloses the paired nasal cavity or the cavity of the nasal capsule (*cav. nc*). The parts of the ethmoidal region situated in front of, between and behind the nasal cavities I will call the prenasal wall, the internasal wall (*w. in*), and the postnasal wall (*w. pn*) respectively; those portions of the ethmoidal region which participate in the formation of the dorsal, ventral and lateral boundaries of the nasal cavity will be termed the roof of the nasal cavity or tectum nasi, the floor or solum nasi (*sol. n*) and the lateral wall of the nasal cavity or the lateral nasal wall. I have regarded the internasal wall as unpaired, the other walls as paired. The prenasal walls of both sides and the median prenasal part of the ethmoidal region situated between the said walls form a continuous skeletal mass, which in the subsequent description must be referred to as a whole. This skeletal mass and its possible derivates will therefore be termed the divisio prenasalis communis (*w. pren*). The postnasal wall is continuous medially with that of the opposite side, while the tectum nasi and solum nasi pass over medially into the internasal wall. The internasal wall may be either entirely solid or may contain cavities. These cavities are of a different nature and position in different groups and have, therefore, been differently termed (e. g. in Urodeles the cavum internasale, in sharks the cavum precerebrale). In those cases where the internasal wall is solid it will be referred to as the septum nasi.

The cavity of each nasal capsule or the nasal cavity (*cav. nc*) comprises either one chamber only or one main chamber and one or more smaller supplementary cavities. These supplementary cavities, here called recesses, have been named by me according to position (e. g. recessus medialis, *re. m*; recessus lateralis, *re. l*) or function (e. g. the recess for the lateral nasal muscle, *re. m. ln*, fig. 52 B). The olfactory organ, which fills the nasal cavity more or less completely, consists of a sack-like formation, the nasal sac (*sac n*, fig. 1). To avoid confusion with the cavity of the nasal capsule I have consistently referred to its cavity as the cavity of the nasal sac (*cav. sac n*). The nasal sac may be developed so as to form one or more diverticles (e. g. diverticulum mediale or the medial diverticle, *di. m*). The cavity of each diverticulum I have called cavum (e. g. cavum mediale, *cav. m*), or if oblong and groove-shaped, sinus (e. g. sinus lateralis, *sin. l*). From either nasal sac an anterior external nasal tube (*nta*) leads to the anterior external nostril (*na*). In addition there is usually a posterior external nasal tube (*ntp*) leading to the posterior external nostril (*np*), and an internal nasal tube or choanal tube (*cht*, fig. 28 A) the aperture of which is the internal nostril or choana (*ch*, fig. 1). The posterior external nasal tube which in Tetrapods functions as the nasolachrymal duct, ductus nasolacrimalis (*dnl*, figs. 19, 29, 30), may be divided in two or more branches. Consequently, there may be one, two (np_1, np_2, figs. 19, 79) or more posterior external nostrils on either side.

The opening in the endocranial nasal capsule through which passes the anterior external nasal tube has been called the fenestra endonarina anterior (*fe. ena*, fig. 1). The opening outside this for the anterior external nasal tube in the dermal skeleton is the fenestra exonarina anterior (*f. exa*). The corresponding openings for the posterior external nasal tube are called the fenestra endonarina posterior (*fe. enp*) and the fenestra exonarina posterior (*fe. exp* or fe_1 *exp* and fe_2 *exp* if there are two) and for the internal nasal tube the fenestra endochoanalis (*fe. ench*) and the fenestra exochoanalis (*fe. exch*). In those cases where there is a common opening for the anterior and posterior external nasal tubes this is named in the endoskeleton the fenestra endonarina communis (*fe. en*, figs. 2, 9, 16) and in the exoskeleton fenestra exonarina communis (*fe. ex*, fig. 33).

As pointed out above (see p. 245), the term lamina nariochoanalis (*la. nch*, fig. 1) has been introduced for that part of the nasal capsule in Rhipidistid Crossopterygians and Amphibians which separates the fenestra endonarina anterior and the fenestra endochoanalis. Pons nariochoanalis refers to the bridge between the anterior external nostril and the choana, formed by the lamina nariochoanalis, dermal bones, and soft tissues.

The anterior part of the orbitotemporal region which in the endocranium follows behind the ethmoidal region, consists of a median wall,

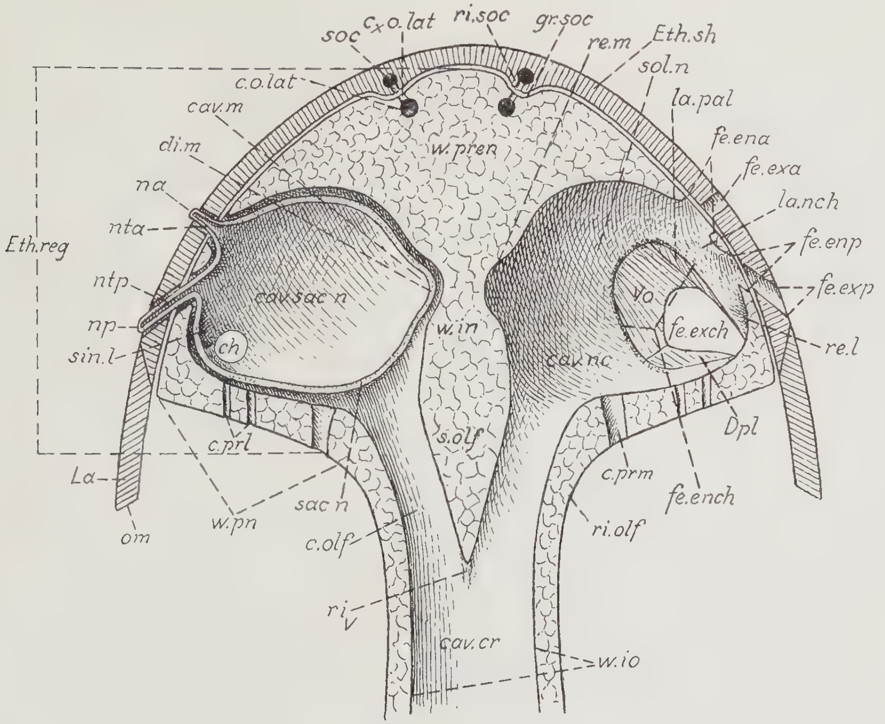

Fig. 1. Diagram showing the general development of the anterior parts of the neural cranium of a Choanate fish in dorsal view. The dorsal parts of the skeleton removed down to the canal for the medial terminal branch of the n. profundus and the fenestra exonarina anterior and fenestra exonarina posterior. On the right side the ventral parts of the cavity of the nasal capsule are shown with the dermal bones participating in the boundary of the fenestra exochoanalis in their approximate position (including the dermopalatine); on the left side the ventral half of the nasal sac with its tubes has been schematically restored. Sutures between the dermal bones of the ethmoidal shield omitted.

Dpl, dermopalatine; *Eth. reg*, ethmoidal region of neural endocranium; *Eth. sh*, ethmoidal shield; *La* lachrymal; *Vo*, vomer; *cav. cr*, cranial cavity; *cav. m*, cavum mediale of cavity of the nasal sac; *cav. nc*, cavity of nasal capsule; *cav. sac n*, cavity of nasal sac; *ch*, choana; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. prl*, *c. prm*, lateral and medial profundus canal; c_x*o. lat*, canal for a branch of r. ophthalmicus lateralis; *di. m*, diverticulum mediale of nasal sac; *fe. ena*, fenestra endonarina anterior; *fe. ench*, fenestra endochoanalis; *fe. enp*, fenestra endonarina posterior; *fe. exa*, fenestra exonarina anterior; *fe. exch*, fenestra exochoanalis; *fe. exp*, fenestra exonarina posterior; *gr. soc*, groove on the upper face of the endocranium for ridge lodging the supraorbital sensory canal; *la. nch*, lamina nariochoanalis; *la. pal*, lamina palatina of the ethmoidal shield; *na*, anterior external nostril; *np*, posterior external nostril; *nta*, anterior nasal tube; *ntp*, posterior nasal tube; *om*, margin of the orbital opening; *re. l*, *re. m*, recessus lateralis and recessus medialis of the cavity of the nasal capsule; *ri. olf*, olfactory ridge; *ri. soc*, ridge on the lower face of the ethmoidal shield, lodging the supraorbital sensory canal; ri_v, median ascending ridge on the floor of cranial cavity; *sac n*, nasal sac; *sin. l*, sinus lateralis of cavity of nasal sac; *soc*, supraorbital sensory canal; *s. olf*, median septum between canales olfactorii; *sol. n*, solum nasi; *w. in*, internasal wall; *w. io*, interorbital wall; *w. pn*, postnasal wall; *w. pren*, divisio prenasalis communis.

the interorbital wall (*w. io*, fig. 1), between the orbits and frequently also of a more or less complete orbital roof, the tectum orbitale (*te. o*, figs. 36, 37) or lamina supraorbitalis (*la. so*, fig. 47). In the interorbital wall lies the cranial cavity (*cav. cr*, fig. 1). The part of the cranial cavity containing the forebrain has been called the forebrain division (*div. fbr*, fig. 57 A). This part of the cranial cavity may be divided into one hemispheral portion (*p. hem*, fig. 57 A—C) and one bulbar portion (*p. bulb*). In certain groups (*Porolepiformes*, *Urodela*) the cranial cavity extends into the ethmoidal region so in these we may discern therein an ethmoidal part (*eth. cr*, figs. 36 A, 38). Through a paired canal the cranial cavity is connected forwards with the nasal cavities. This canal has been called the canalis olfactorius (*c. olf*, fig. 1), even though it contains, beside the olfactory nerve, certain other parts of the brain (bulbus olfactorius, lobus olfactorius). In some forms the canalis olfactorius may be so considerably shortened as to constitute a fenestration only, the fenestra olfactoria (*fe. olf*, fig. 16 C), in the thin wall which in these forms divides the cranial and the nasal cavities.

Foramina, canals, grooves, etc., have as a rule been called after the vessels, nerves or other formations that pass or, in fossil forms, may be assumed to have passed through them (e. g. the canal for the r. ophthalmicus lateralis, *c. o. lat.* fig. 1). In certain cases a shorter name, e. g. the profundus canal instead of the canal for the n. profundus, has been used.

In many Devonian Gnathostomes both the endocranium and the visceral endoskeleton are strongly and extensively ossified. Even during the Devonian and later on during subsequent geological periods a regressive development took place in the ossifications of the endoskeleton within the various groups (Stensiö 1921, pp. 271—274; 1922, p. 198; 1922 a, pp. 1259—1269; 1925, p. 182; 1925 a, pp. 161—163; 1932, pp. 20, 21, 297; 1934, p. 66; Case 1933; Holmgren and Stensiö 1936, pp. 235—239). This regressive development which proceeded independently in the various groups, caused a secondary progressive "chondrification". The original endoskeletal ossifications were gradually secondarily replaced by cartilage or were divided into a number of minor ossifications which in turn secondarily "chondrified". The minor ossifications thus developed cannot with certainty be homologized in the different phyletic lines. Under these circumstances I have not been able to introduce a common terminology for the cartilage-bones of the snout. The terms hitherto used for the cartilage-bones in different groups have on the whole been maintained. However, in a few instances I have found the earlier names less suitable. The paired ossification in the ethmoidal region of the Coelacanthids, *Brachiopterygii* (*Polypterus*) and sturgeons I have simply called the ethmoidal ossification (cf. MOY-THOMAS 1937, p. 388) as I have not wished here to take up an attitude towards the question of their homologues in various groups. The bone in Urodeles which has hitherto in the literature been called the septomaxillary is, as will be demonstrated below, a cartilage-bone in the lateral wall of the nasal cavity. This being the case the opinion so far generally held (GAUPP 1905, p. 746; FUCHS 1911; WEGNER 1922; STADTMÜLLER 1936, pp. 622—624; cf. DE BEER 1937, p. 442) cannot be maintained, viz. that it is homologous to the septomaxillary in *Anura* and reptiles. For this cartilage-bone in Urodeles I have proposed the term nariodal. For the dermal bone occurring in approximately the corresponding place in *Anura* and reptiles the term septomaxillary has been kept.[1]

As the dermal bones have not been thoroughly treated in this work, I have as a rule avoided questions regarding the nomenclature of the dermal bones. I have retained the names of dermal bones generally accepted although in many instances they could be subjected to well-founded criticism (see pp. 343—346). On the snout of Crossopterygians there are laterally to the nasal series a number of dermal bones primarily not pierced by any sensory canals. For these dermal bones, hitherto not very well known and incorrectly called antorbitals, the name tectals has been introduced, this with reference to the position of these bones on the roof of the nasal cavity (tectum nasi).

As is well-known, the cranium of Crossopterygians is divided into one anterior and one posterior part. In an earlier paper (JARVIK 1937) I have called these two parts the divisio cranialis anterior and the divisio cranialis posterior respectively. The divisio cranialis anterior comprises the ethmosphenoid (or its derivates), the fronto-ethmoidal shield (the anterior part of the dermal skull-roof from the tip of the snout backwards as far as to the hinder ends of the frontals), the vomers, and the parasphenoid. The divisio cranialis posterior consists of the otico-occipital (or its derivates), the parietal shield (the posterior part of the dermal skull-roof composed of the parietals, intertemporals and supratemporals), and the extrascapular series of bones. The palatoquadrate and its dermal bones (dermopalatine, ectopterygoid and entopterygoid) constitute together the palatoquadrate complex. The larger unity formed both by the said complex and by the dermal bones of the cheek was called the palatoquadrate-cheek complex.

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[1] Instead of septomaxillary (W. K. PARKER 1871) several authors (STADTMÜLLER, CHUNG, REINBACH) use the name nariale introduced by WEGNER (1922). Most scientists (DE BEER, DE VILLIERS, DU TOIT, GOODRICH, LAPAGE, NOBLE, RAMASWAMI, ROMER, SÄVE-SÖDERBERGH, VERSLUYS, and others) however still use septomaxillary, a name that is to be preferred for reasons of priority.

III. Review of the snout in certain recent forms.

A. Elasmobranchs, with special reference to Chlamydoselachus.

As a type of the sharks I have chosen *Chlamydoselachus* (figs. 2—4). This form is now quite well known (Allis 1923; Gudger and Smith 1933; B. G. Smith 1937; Holmgren 1941). *Chlamydoselachus* is certainly one of the most primitive of the recent sharks (B. G. Smith 1937, p. 495, foot-note 1), for which reason it is well suited for a comparison with the Crossopterygians described below. As shown by Stensiö (1937) and Gross (1937, 1938), *Chlamydoselachus* must be closely related to the Devonian *Cladodus.*

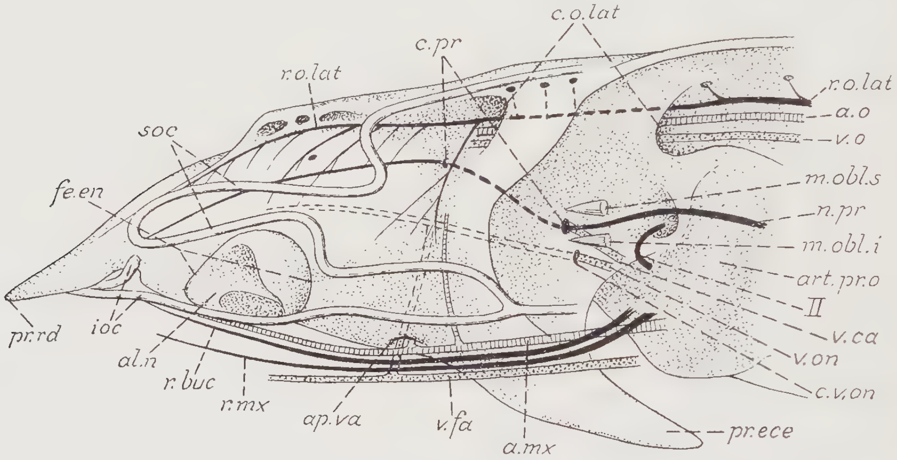

Fig. 2. *Chlamydoselachus anguineus.* Diagram of the anterior part of the endocranium with nerves, vessels and sensory canals. Lateral view. Compilation after the descriptions and figures given by Allis (1923).

al. n, ala nasalis; *a. mx,* maxillary artery; *a. o,* ophthalmic artery; *ap. va,* aperture for vessels; *art. pr. o,* facet for the articulation of the processus orbitalis; *c. o. lat,* canal for the r. ophthalmicus lateralis; *c. pr,* profundus canal; *c. v. on,* canal for the orbitonasal vein; *fe. en,* fenestra endonarina communis (anterior + posterior); *ioc,* infraorbital sensory canal; *m. obl. i, m. obl. s,* m. obliquus inferior and m. obliquus superior; *n. pr,* n. profundus; *pr. ece,* ectethmoid process; *pr. rd,* dorsal rostral process; *r. buc,* r. buccalis lateralis; *r. mx,* r. maxillaris V; *r. o. lat,* r. ophthalmicus lateralis; *soc,* supraorbital sensory canal; *v. ca,* anterior cerebral vein; *v. fa,* anterior facial vein; *v. o,* ophthalmic vein (not always present); *v. on,* orbitonasal vein; *II,* n. opticus.

With regard to the structure of the snout in certain other Elasmobranchs see below (pp. 388—389).

The ethmoidal region of *Chlamydoselachus* (figs. 2—4) covers a good third of the whole length of the endocranium and is, consequently, comparatively long. The two cartilaginous nasal capsules lie far apart so the internasal wall is wide. The skeleton of the internasal wall is composed, besides of the two thin medial walls of the nasal cavities, of a thin, wide, almost horizontal cartilaginous plate only, the internasal lamina (*la. in*). This lamina forms the bottom of a chamber in the internasal wall, the cavum precerebrale (*cav. prec*), which opens upwards and forwards. Laterally this chamber is bounded by the dorsal parts of the medial walls of the nasal cavities. Backwards it is connected by a wide opening, the fenestra precerebralis (*fe. prec*), with the cranial cavity. ALLIS (1913, pp. 322—323; 1923, p. 128) homologizes the cavum precerebrale and the fenestra precerebralis to the cavum internasale and the fenestra precerebralis respectively in Urodeles (see pp. 286, 382, 400). On the lower side of the internasal lamina there is a wide shallow pit, the subethmoidal depression (ALLIS 1923, p. 126), bounded laterally by the ventral parts of the nasal capsules and backwards by the most posterior descending part of the internasal lamina. In other sharks, e. g. *Squalus* (HOLMGREN and STENSIÖ 1936, fig. 239 B), the internasal lamina is provided on its lower side with a median keel. The basal communicating canal occurring in many sharks (see HOLMGREN and STENSIÖ 1936, pp. 305—306, 308) is absent in *Chlamydoselachus*. This canal, the existence of which according to HOLMGREN and STENSIÖ (1936, p. 306) is dependent on the relative size of the nasal capsules, is a special formation. The internasal lamina is continued in *Chlamydoselachus* in front of the nasal capsules by a broad short process, the dorsal rostral process (*pr. rd*; cf. below, p. 258). This process which together with the prenasal walls of both sides constitutes the divisio prenasalis communis is on either side separated from the nasal capsules by a deep incisure. Close ventrally to the rostral process lies on either side the foremost part of the infraorbital sensory canal (*ioc*) which is bent like a hairpin and has its anterior end immediately dorsolaterally to the incisure already mentioned.

The nasal cavity is surrounded by thin walls. It opens outwards in two large openings, the fenestra endonarina and the nasal fontanelle, and backwards to the cranial cavity through the canalis olfactorius. The fenestra endonarina (*fe. en*, figs. 2, 4), which is to be regarded as a fenestra endonarina communis (anterior + posterior), is situated in the anterior part of the lateral wall that faces antero-ventro-laterally. By a cartilage, the ala nasalis (*al. n*), it is divided into one antero-lateral (the fenestra endonarina anterior) and one postero-medial (the fenestra endonarina posterior) portion for the incurrent and excurrent external nasal apertures respectively. The nasal fontanelle (*font. n*) lies in the floor[1] of the nasal cavity, postero-medially to the fenestra endonarina, from which it is separated by a cartilaginous bridge. As pointed out by ALLIS (1923, p. 132), this fontanelle occupies a position corresponding to that of the fenestra endochoanalis (fenestra choanalis) in Amphibians and is, in his opinion, homologous to this (see below, p. 383). The cartilaginous bridge between it and the fenestra endonarina would thus represent the lamina nariochoanalis. Apart from a small opening (*ap. va*) for vessels in its posterolateral corner, the nasal fontanelle is closed by a membrane. No choanal tube passes through it. No choanal tube exists in adult sharks and, as far as I have been able to ascertain in the literature (HOLM 1895; PETER 1901; BERLINER 1902; SUND 1904; MATTHES 1934), no evidence of such a tube has been found in shark embryos either.

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[1] DE BEER's (1937, p. 456) assertion that the nasal cavity in sharks is devoid of a floor is untenable from a morphological point of view.

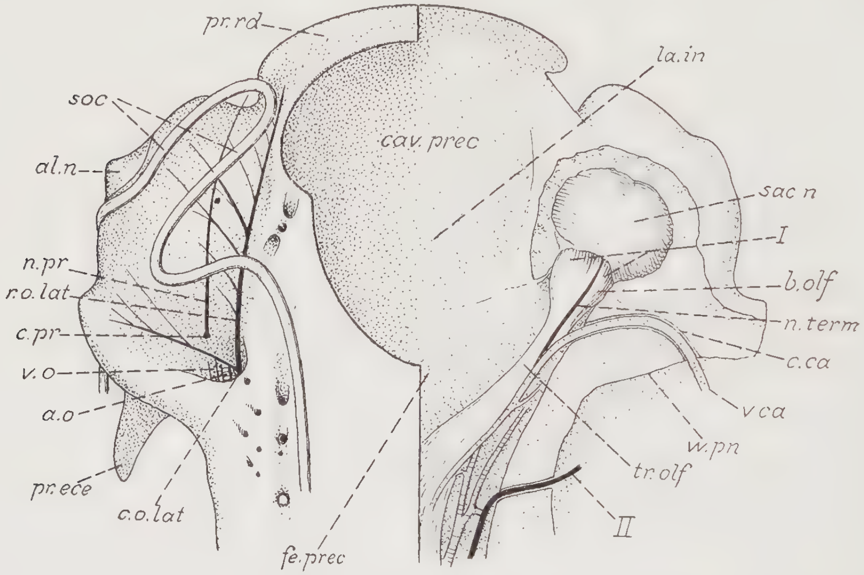

Fig. 3. *Chlamydoselachus anguineus.* Diagram of the anterior part of the endocranium with nerves, vessels, and sensory canals in dorsal view. Dorsal parts of the cartilage of the right side removed. Compilation after the descriptions and figures given by ALLIS (1923).

al. n, ala nasalis; *a. o,* ophthalmic artery; *b. olf,* bulbus olfactorius; *cav. prec,* cavum precerebrale; *c. ca,* canal for anterior cerebral vein; *c. o. lat,* canal for r. ophthalmicus lateralis; *c. pr,* profundus canal; *fe. prec,* fenestra precerebralis; *la. in,* lamina internasalis; *n. pr,* n. profundus; *n. term,* n. terminalis; *pr. ece,* ectethmoid process; *pr. rd,* dorsal rostral process; *r. o. lat.* r. ophthalmicus lateralis; *sac n,* nasal sac; *soc,* supraorbital sensory canal; *tr. olf,* tractus olfactorius; *v. ca,* anterior cerebral vein; *v. o,* ophthalmic vein (not always present); *w. pn,* postnasal wall; *I,* n. olfactorius; *II,* n. opticus.

The postnasal wall (*w. pn*) in *Chlamydoselachus* is well developed and pierced by several canals for nerves and vessels. Its postero-ventrolateral corner is extended into a process directed postero-ventro-laterally, the ectethmoid process (*pr. ece*, the "antorbital cartilage"; HOLMGREN 1941, p. 7; figs. 6, 7), the lower edge of which is coated with tough connective tissue against which slides the processus palatinus of the palatoquadrate.

The nasal sac (*sac n*) in *Chlamydoselachus* does not seem to have been fully described (cf. B. G. SMITH 1937, p. 487). Judging from figures given by ALLIS (1923, pl. 22, fig. 59) and B. G. SMITH (1937, pl. 6, fig. 24) it is probably incompletely divided by a groove into one lateral and one medial rounded part, very much as in *Heptanchus* (DANIEL 1934, fig. 200 A; cf. fig. 45 B below). It is connected with the bulbus olfactorius (*b. olf*) by the short nervus olfactorius (*I*) which is divided into two portions. The tractus olfactorius (*tr. olf*) is comparatively long. The bulbus olfactorius lies with the olfactory nerve in the short canalis olfactorius, whereas the tractus olfactorius is situated in the cranial cavity.

The r. ophthalmicus lateralis (*r. o. lat*) is enclosed in a fairly long canal, *c. o. lat* (by most authors called the preorbital canal), which pierces the dorso-medial part of the postnasal wall. The funnel-shaped posterior opening of this canal lies fairly far posteriorly in the orbit. The anterior opening of the canal is on the upper surface of the postero-medial part of the tectum nasi. After emerging from the canal *c. o. lat*, the r. ophthalmicus lateralis goes forwards dorsally to the medial part of the nasal capsule. Thus it does not enter the nasal cavity.

The r. ophthalmicus lateralis in *Chlamydoselachus* is accompanied in the snout by a general cutaneous branch. The latter branch which may either be fused with the r. ophthalmicus lateralis (ALLIS) or form an independent nerve (HAWKES) was referred to by HAWKES (1906, p. 972) as the r. ophthalmicus superficialis V. According to ALLIS (1923, p. 211), however, it probably represents the portio ophthalmici profundi (or r. frontalis profundi; cf. GOODRICH 1930, p. 750). It is not known whether any real r. ophthalmicus superficialis V is developed in *Chlamydoselachus*. In *Squalus* (NORRIS and HUGHES 1920, p. 332, fig. 51) and *Heptanchus* (DANIEL 1934, p. 223) such a nerve exists though very poorly developed. It is in *Squalus* distributed only to the skin dorsally to the orbit and thus hardly reaches the snout. Since all the general cutaneous fibres found in the dorsal parts of the snout of *Chlamydoselachus* probably belong to the n. profundus, it is very likely that the r. ophthalmicus superficialis V, if at all developed, in this form (as in *Squalus* and presumably in Selachians in general) goes no farther forwards than up to about the anterior part of the orbit.

In Gnathostomes in general (cf. pp. 263, 268, 282, 302) the r. ophthalmicus superficialis V is normally so closely associated with the portio ophthalmici profundi and the r. ophthalmicus lateralis, that it is difficult to determine how far forwards the sensory fibres belonging to the trigeminus proper actually reach (NORRIS 1925, pp. 360—362; GOODRICH 1930, p. 751; HALLER v. HALLERSTEIN 1934, pp. 570—582). As it cannot be stated for certain that the r. ophthalmicus superficialis V in Gnathostomes participates in the innervation of the preorbital part of the head, I have in this paper described all the nerves in the dorsal parts of the snout which are composed of general cutaneous fibres as belonging to the n. profundus.

The n. profundus[1] (*n. pr*, figs. 2, 3) in *Chlamydoselachus* traverses a fairly long canal, the profundus canal (*c. pr*). The posterior orifice of this canal lies approximately in the middle of the posterior face of the postnasal wall while the anterior orifice is on the upper side of the tectum nasi, antero-laterally to the anterior orifice of the canal for the r. ophthalmicus lateralis. On leaving the profundus canal the n. profundus runs forwards above the nasal capsule dividing into branches which supply the skin on the dorsal side of the snout. According to MORI (1924, p. 399) two small profundus branches come from above into the posterior part of the nasal cavity in *Squalus*. These two branches divide in the nasal cavity into a number of twigs which leave it again through openings in the lateral wall. As is evident from the descriptions and figures given by NORRIS and HUGHES (1920, p. 331, figs. 2—4), however, in *Squalus* the main portion of the n. profundus does not enter the nasal capsule. The same applies to *Heptanchus* (DANIEL 1934, p. 223) and *Mustelus* (ALLIS 1901, p. 159). From what has been said above it is clear that the n. profundus in sharks, with the exception of insignificant twigs, does not enter or pass through the nasal cavity.[2] A characteristic feature of the n. profundus in sharks is further that it does not bifurcate into one lateral and one medial nasal branch and that it does not anastomose with the r. maxillaris V or the r. palatinus VII.

The r. maxillaris V (*r. mx*) and the r. buccalis lateralis (*r. buc*) cross the dorso-lateral side of the ectethmoidal process, thence continuing forwards ventro-medially to the fenestra endonarina, beneath the cartilaginous bridge that separates this from the nasal fontanelle. Neither in *Chlamydoselachus* nor in *Squalus* do they enter the nasal cavity.

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[1] This refers only to the ventral branch (r. ophthalmicus profundus or r. nasalis; cf. GOODRICH 1930, p. 750) of the n. profundus. The dorsal branch (r. frontalis or portio ophthalmici profundi), the development of which is considerably weaker, accompanies the r. ophthalmicus lateralis.

[2] Acc. to GEGENBAUR and HOFFMANN (see ISELSTÖGER 1937, pp. 374—375) the n. profundus in rays enters the nasal cavity together with the r. ophthalmicus lateralis.

The r. maxillaris V is in *Chlamydoselachus* accompanied by what Allis (1923, p. 132; pl. 20, fig. 55, *ecmx*) calls the maxillary branch of the external carotid artery (*a. mx*, figs. 2, 4; cf. Goodrich 1930, pp. 514—516). After crossing the ectethmoid process on the dorsolateral side, this artery gives off two dorsal branches. One of these runs upwards on the outside of the nasal capsule while the other enters the nasal cavity through the opening *ap. va* in the membrane that closes the nasal fontanelle. Other arterial branches (*a. o*), by Allis (1923, p. 146) called the ophthalmic branches of the external carotid artery (corresponding to the rostral artery in *Mustelus*, T. J. Parker 1886, p. 695, and the superior orbital artery in *Squalus*, O'Donoghue and Abbot 1928, p. 843), accompany the r. ophthalmicus lateralis through the postnasal wall. It is uncertain whether, as stated by Corrington

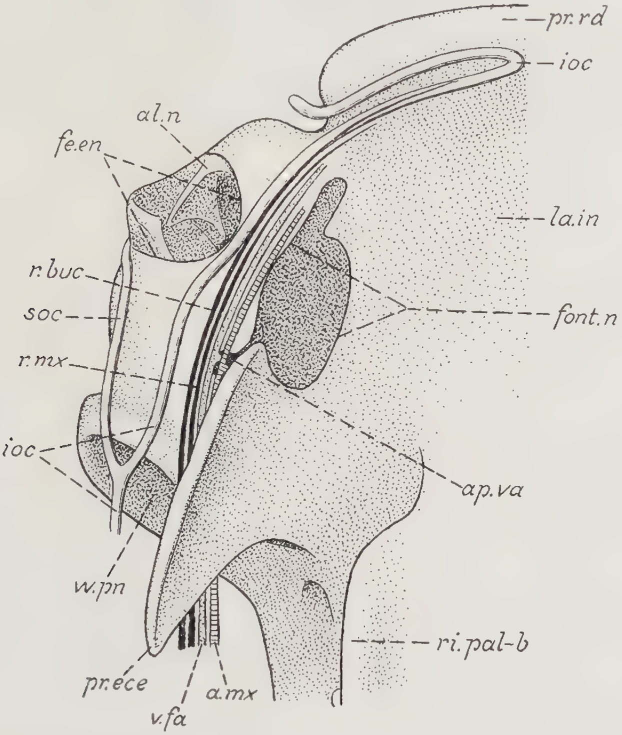


Fig. 4. *Chlamydoselachus anguineus.* Right half of the anterior part of the endocranium with nerves, vessels, and sensory canals in ventral view. Compilation after the descriptions and figures given by Allis (1923).

al. n, ala nasalis; *a. mx,* maxillary artery; *ap. va,* aperture for vessels; *fe. en,* fenestra endonarina communis; *font. n,* nasal fontanelle; *ioc,* infraorbital sensory canal; *la. in,* lamina internasalis; *pr. ece,* ectethmoid process; *pr. rd,* dorsal rostral process; *r. buc,* r. buccalis lateralis; *r. mx,* r. maxillaris V; *ri. pal-b,* palato-basal ridge; *soc,* supraorbital sensory canal; *v. fa,* facial vein; *w. pn,* postnasal wall.

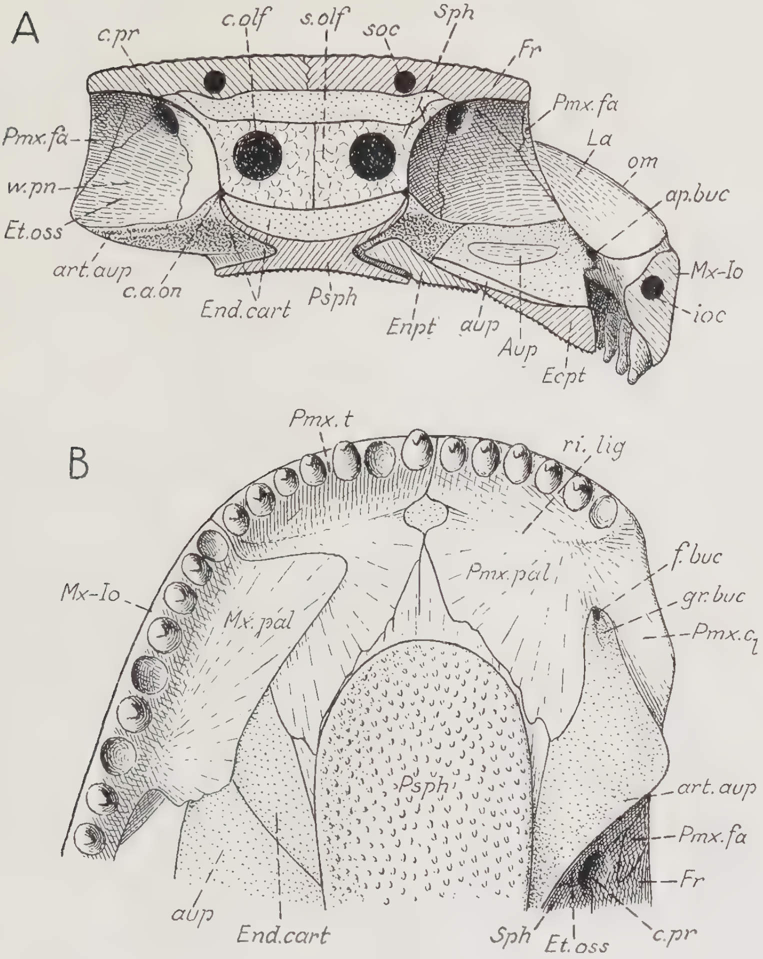
(1930, p. 244; cf. Daniel 1934, p. 182; Holmgren and Stensiö 1936, p. 301), there is an artery in *Chlamydoselachus* which passes the so-called orbitonasal canal (the canal for the orbitonasal vein, *c. v. on*, fig. 2). As far as I have been able to find, Allis (1911, 1916, 1923) does not mention any such artery. On the other hand, the artery called by Allis the "orbital" artery (a branch of the external carotid) gives off a small twig which runs "across the floor of the orbit onto the ventral surface of the preorbital portion of the chondrocranium" (Allis 1911, p. 517). This inconsiderable artery has been omitted in the figures given in this work.

The most important veins draining the snout of *Chlamydoselachus* (Allis 1923, p. 203) are the anterior facial vein (*v. fa*), which accompanies the maxillary branch of the external carotid, and the orbitonasal vein (*v. on*) coming from the postero-ventro-medial part of the nasal cavity (the ectethmoidal chamber, Allis). The latter vein, which Allis (1923, p. 133) homologizes to the v. orbitonasalis in *Rana*, pierces the postnasal wall in a canal (*c. v. on*) the posterior opening of which lies but slightly ventrally to the orbital orifice of the profundus canal. In the nasal cavity the orbitonasal vein anastomoses with the anterior facial vein. This anastomosis passes the opening *ap. va* together with the branch of the maxillary artery that enters the nasal cavity. Further, there is presumably (cf. Allis 1923, pp. 146 and 203) a third vein leading from the dorso-medial parts of the snout, the ophthalmic vein (*v. o*), which probably goes through the canal (*c. o. lat*) for the r. ophthalmicus lateralis. According to Daniel (1934, pp. 205—206, fig. 192 A) a supraorbital vein is found in *Squalus* dorsally to the cranial roof. After receiving one dorso-medial and one dorso-lateral rostral branch this supraorbital vein enters the nasal cavity through a foramen in the tectum nasi continuing there as the nasomaxillary vein.

The vena cerebralis anterior (*v. ca*) in *Chlamydoselachus* leaves the cranial cavity together with the tractus olfactorius and then goes in a curved canal (*c. ca*, fig. 3) laterally and backwards to the orbit. The orbital orifice of this canal lies very near or coincides with the orbital orifice of the profundus canal.

B. **Brachiopterygii (Polypterus) Stensiö 1921.**

In *Polypterus* (figs. 5—9, 84, Bridge 1888; Pollard 1892; Winslow 1898; Allis 1900, 1900 a, 1919 a, 1922; Budgett 1902; Lehn 1918; Moy-Thomas 1933; Holmgren and Stensiö 1936; De Beer 1937) the ethmoidal region is comparatively short. As the postnasal wall (*w. pn*, figs. 5, 6, 7, 9) is so orientated as to have its orbital face rather much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c.pr

Fig. 5. *Polypterus senegalus.* Skeleton of snout with the palatoquadrate-cheek complex removed on the left side. *A*, in posterior, and, *B*, in ventral view. In *B*, dermal bones of the palatoquadrate removed. Cartilage dotted. After a specimen in the Swedish Museum of Natural History. $^{4}/_{1}$.

Aup, autopalatine; *Ecpt,* ectopterygoid; *End. cart,* cartilage of endocranium; *Enpt,* entopterygoid; *Et. oss,* ethmoidal ossification ("ectethmoid"); *Fr,* frontal; *La,* lachrymal; *Mx-Io,* maxillo-jugal ("maxillary-infraorbital"); *Mx. pal,* palatal lamina of maxillo-jugal; *Pmx.* c_{l}, rostro-caudal sensory canal component of compound "premaxillary" (probably tecto-rostro-premaxillary); *Pmx. fa,* facial portion of compound "premaxillary"; *Pmx. pal,* palatal lamina of compound "premaxillary"; *Pmx. t,* premaxillary portion of the compound "premaxillary"; *Psph,* parasphenoid; *Sph,* ossified part of the interorbital wall ("sphenoid"); *ap. buc,* opening for r. buccalis lateralis, r. maxillaris V and vessels; *art. aup,* articular area for pars autopalatina palatoquadrati; *aup,* cartilage of pars autopalatina palatoquadrati; *c. a. on,* canal for orbitonasal artery (posterior opening); *c. olf,* canalis olfactorius; *c. pr,* profundus canal; *f. buc, gr. buc,* foramen and groove for r. buccalis lateralis, r. maxillaris V and vessels; *ioc,* infraorbital sensory canal; *om,* margin of orbital opening; *ri. lig,* ridge for attachment of ligaments; *soc,* supraorbital sensory canal; *s. olf,* median septum between canales olfactorii; *w. pn,* postnasal wall.

postero-laterally directed, the region attains its greatest width about midway between its anterior and posterior ends. The greater part of the region consists of cartilage. Only a fairly small paired ossification is developed in it (*Et. oss*, figs. 5, 7, 9; ectethmoid ALLIS, HOLMGREN and STENSIÖ). This ossification is in such a position as to form the main part of the postnasal wall as well as an adjoining postero-lateral part of the floor of the nasal cavity. Posteriorly it is connected by a suture with the paired so-called sphenoid bone (*Sph*, figs. 5, 7).

The oblong nasal cavities are separated by a thin cartilaginous nasal septum (*sn*, fig. 7) which has a posterior continuation (*s. olf*) between the canales olfactorii (*c. olf*), a continuation which may in some species be wide (fig. 5 A; cf. BING and BURCKHARDT 1905, fig. 30), in others comparatively narrow (fig. 7), and which is made up of the medial parts of the sphenoid bones, with the exception of the antero-dorsal part which is cartilaginous. Anteriorly the nasal septum is continuous with the divisio prenasalis communis (*w. pren*, fig. 7), which is strongly developed. In the fully developed *Polypterus*, the median part of the divisio prenasalis communis is produced forwards into a wide, but rather thin unpaired process, the ventral rostral process (*pr. rv*, figs. 6, 7, 9; rostral process, ALLIS; rostrum, DE BEER), lying just ventrally to the ethmoidal commissure of the infraorbital sensory canals (*ioc*, fig. 84). In older larvae (POLLARD, LEHN, WINSLOW), however, we find at the rostral end of the divisio prenasalis communis one dorsal (*pr. rd*, fig. 6 B) and one ventral lamina (*pr. rv*) separated by a fairly deep, transverse groove for the ethmoidal commissure of the infraorbital canals. Of these two laminae the dorsal one, the dorsal rostral process, stops, however, in its development and is hardly discernible in the adult, while the ventral one, which in the larvae is but slightly longer than the dorsal one, increases considerably and persists as the definite (ventral) rostral process of the adult. The so-called rostral process in *Chlamydoselachus* (*pr. rd*, figs. 2—4) lies immediately dorsally to the most anterior parts of the infraorbital sensory canals[1] and thus it is probably most nearly comparable to the dorsal lamina in the *Polypterus* larva, for which reason it has above (p. 251) been called the dorsal rostral process. The conditions in the *Polypterus* larva show that no very great importance can be attached to the position of the ethmoidal commissure in relation to the rostral tip of the endocranium (cf. below p. 601).

In *Polypterus* the walls of the nasal cavity are almost complete. The fenestra endonarina (*fe. en*, figs. 6 B, 7, 9) is fairly large and situated in the anterior part of the lateral wall of the cavity. In addition to vessels and nerves (fig. 9) this fenestra gives passage to both the anterior (*nta*) and posterior (*ntp*) nasal tubes (fig. 7). It is thus a fenestra endonarina communis (fenestra endonarina anterior + posterior).

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[1] The two infraorbital sensory canals in *Chlamydoselachus* come into contact at the median line, but according to ALLIS (1923, p. 196) it is uncertain whether they form an actual anastomosis there.

Outside the fenestra endonarina communis we find a fairly large opening, the fenestra exonarina communis, in the dermal skeleton, which is incompletely separated by the terminal bone (*Term*, fig. 84) into a fenestra exonarina anterior (*fe. exa*) for the anterior external nasal tube and a fenestra exonarina posterior (*fe. exp*) for the posterior external nasal tube.

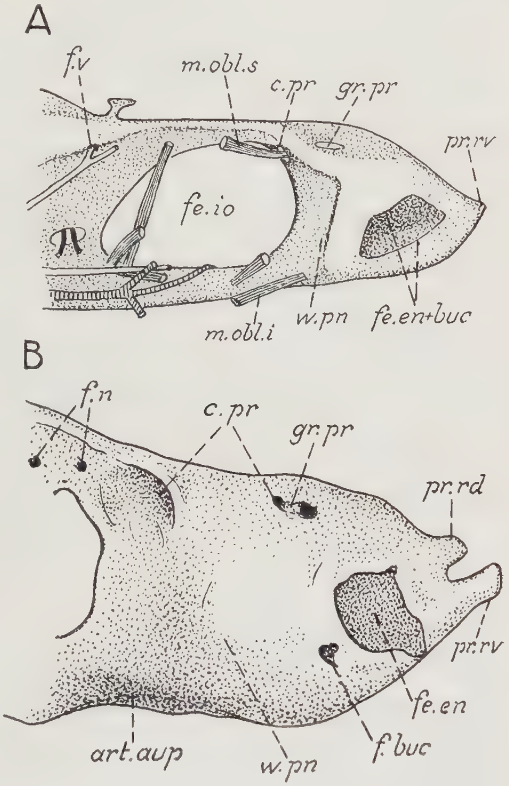

Fig. 6. *Polypterus senegalus.* The anterior part of the endocranium in lateral view. *A*, 30 mm larva. From Moy-Thomas (1933, fig. 11). $^{20}/_{1}$. *B*, 76 mm larva. From Lehn (1918, fig. 3). $^{19}/_{1}$.

art. aup, articular area for pars autopalatina; *c. pr*, profundus canal; *f. buc*, foramen for r. buccalis lateralis, r. maxillaris V, and vessels; *fe. en*, fenestra endonarina communis; *fe. en + buc*, fenestra endonarina communis and foramen for r. buccalis before separation; *fe. io*, interorbital fenestra; *f. n*, foramina for nerve branches; *f. v*, foramen for vein branch; *gr. pr*, groove for the n. profundus, r. maxillaris V, and vessels; *m. obl. i*, m. obliquus inferior; *m. obl. s*, m. obliquus superior; *pr. rd*, *pr. rv*, dorsal and ventral rostral process; *w. pn*, postnasal wall.

Somewhat behind and beneath the fenestra endonarina communis there is a small opening, *f. buc* (figs. 5 B, 6 B, 7, 9), in the lateral wall of the nasal cavity for vessels and nerves. From this opening a short groove, *gr. buc* (fig. 5 B), leads backwards on the ventral surface of the ethmoidal region. As regards position the foramen *f. buc* reminds of the foramen *ap. va* (figs. 2, 4) for vessels in the membrane closing the nasal fontanelle in *Chlamydoselachus*. While the opening *ap. va* in *Chlamydo-*

selachus constitutes the postero-lateral part of the nasal fontanelle, the opening *f. buc* in *Polypterus* must be regarded as a part of the fenestra endonarina communis bounded off from this fenestra comparatively late during the embryonic development by a cartilaginous bridge. That this must be the case is apparent from a comparison between Moy-Thomas' figures (1933, figs. 11 and 12) of a 30 mm stage and Lehn's figures (1918, figs. 2 and 3) of a 76 mm stage. What evidently becomes the opening *f. buc* in the 76 mm stage (fig. 6 B) and in the adult, forms part of the fenestra endonarina communis (*fe. en + buc*) in the 30 mm stage (fig. 6 A). *Polypterus* is both in larvae and adults devoid of an opening comparable to the antero-medial, larger part of the nasal fontanelle in *Chlamydoselachus* which is a fenestra in the floor of the nasal cavity.

The postnasal wall in *Polypterus* is pierced in its dorso-medial part by the profundus canal (*c. pr*, figs. 5, 6, 9) which gives passage both to the n. profundus and to, inter alia, also the r. ophthalmicus lateralis. The orbital opening of this canal widens funnellike for the m. obliquus superior (*m. obl. s.* figs. 6 A, 9) which penetrates into the canal and attaches itself to its medial wall. The canal emerges on the upper side of the ethmoidal region where it is continued forwards by a distinct groove (*gr. pr*, figs. 6, 9) leading a short distance forwards to a foramen in the roof of the nasal cavity. From the anterior part of the lateral face of the orbitotemporal region, immediately above the upper lateral margin of the parasphenoid, a canal for the orbitonasal artery (*c. a. on*, figs. 5 A, 7, 9) runs forward through the interorbital wall opening anteriorly into the canalis olfactorius (*c. olf*). Some distance antero-laterally to the orbital (posterior) orifice of the last-mentioned canal there is, at least in the larvae described by Lehn (1918, p. 385), a large pit in the very lowest part of the posterior (orbital) face of the postnasal wall. This pit is the place of origin of the m. obliquus inferior (*m. obl. i*, figs. 6 A, 9). Immediately in front of the said pit lies the articular area (*art. aup*, fig. 6 B) for the pars autopalatina of the palatoquadrate. In adults this articular area (fig. 5) is extended further laterally and is more groove-like than in the larvae. It is only the dorsal margin of the foremost part of the pars autopalatina palatoquadrati that slides against it.

The paired canalis olfactorius (*c. olf*, figs. 5 A, 7) is relatively long and, at least sometimes (cf. figs. 5 A and 8), of greater height than width. The nasal cavity (*cav. nc*, fig. 7; cf. fig. 8, *sac n*) is almost oviform. In its anterior part it exhibits two recesses, one antero-lateral and one antero-medial. Of these the antero-lateral one lies just medially to the fenestra endonarina communis and houses the diverticle of the nasal sac from which issue the two nasal tubes, while the antero-medial recess (*re. am*, fig. 7) is developed for an antero-medial diverticle of the nasal sac.

The external shape of the nasal sac (*sac n*, figs. 7, 8; Waldschmidt 1887; Bing and Burckhardt 1905, fig. 30; Wiedersheim 1909, pp. 375—376; Allis 1922, pp. 198—199; Marcus 1930, pp. 683—686;

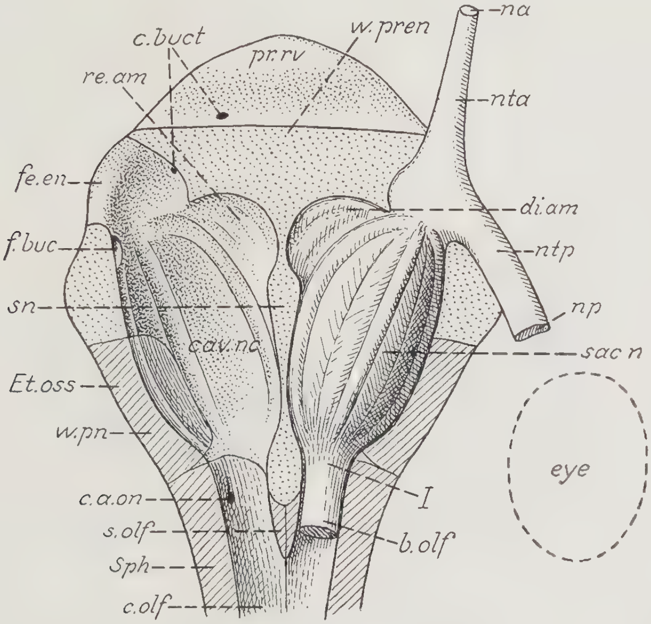

Fig. 7. *Polypterus bichir.* Ethmoidal region and anterior part of the orbitotemporal region of the endocranium in dorsal aspect. The dorsal parts removed so as to show the left nasal cavity and the right nasal sac. Cartilage dotted. After a specimen in the Swedish Museum of Natural History. $^5/_2$.

Et. oss, "ectethmoid"; *Sph,* "sphenoid"; *b. olf,* bulbus olfactorius; *c. a. on,* canal for orbitonasal artery (anterior opening); *cav. nc,* cavity of nasal capsule; *c. buct,* canal for terminal portion of r. buccalis lateralis; *c. olf,* canalis olfactorius; *di. am,* antero-medial diverticle of nasal sac; *f. buc,* foramen for r. buccalis lateralis, r. maxillaris V, and vessels; *fe. en,* fenestra endonarina communis; *na,* anterior external nostril; *np,* posterior external nostril; *nta, ntp,* anterior and posterior nasal tubes, respectively; *pr. rv,* ventral rostral pocess; *re. am,* antero-medial recess of the cavity of the nasal capsule; *sac n,* nasal sac; *sn,* septum nasi; *s. olf,* median septum between canales olfactorii; *w. pn,* postnasal wall; *w. pren,* divisio prenasalis communis; *I,* n. olfactorius.

Matthes 1934, p. 891) greatly resembles that of the nasal cavity and it is thus almost oviform. It is generally divided into five sectors by five longitudinal septa. The n. olfactorius enters the sac at its posterior end and runs forward in the solid central part of the sac, giving off branches in all directions. The anterior part of the nasal sac protrudes so as to form an antero-medial diverticle (*di. am*) which, as already mentioned, lies in the antero-medial recess of the nasal cavity.

The anterior and posterior nasal tubes issue from a small common diverticle of the foremost part of the nasal sac, laterally to and in front of the antero-medial diverticle. The anterior nasal tube (*nta*) goes forwards while the posterior nasal tube takes a backward course in the skin ending just in front of the eye. Because of this diverging course of the nasal tubes the anterior (*na*) and posterior (*np*) external nostrils are situated rather far from the fenestra exonarina anterior and posterior respectively. The olfactory nerve (*I*, figs. 7, 8) is short and occupies the anterior part of the canalis olfactorius only. The posterior part of this canal lodges the high and narrow bulbus olfactorius (*b. olf*) which lies just in front of the hemisphere of the forebrain (Waldschmith 1887; cf. Holmgren 1922, pp. 422—426; Kappers 1934, p. 446). Owing to its position in the posterior part of the canalis olfactorius the bulbus olfactorius is separated from that of the opposite side by the posterior extension (*s. olf*) of the septum nasi.

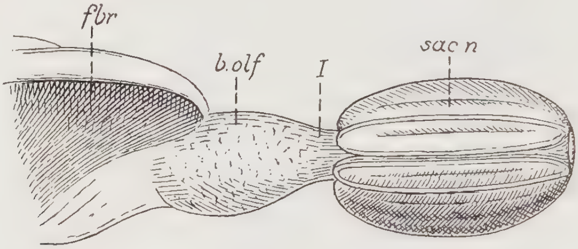

Fig. 8. *Polypterus bichir*. Anterior part of the brain with the right nasal sac in lateral view. Young animal. × $^5/_1$ approximately. From Waldschmidt (1887, fig. 3).

b. olf, bulbus olfactorius; *fbr*, forebrain; *sac n*, nasal sac; *I*, n. olfactorius.

The course of the principal nerves and vessels in the snout of *Polypterus* is shown schematically in fig. 9, which is, in the main, based on the descriptions and figures given by Allis (1922).

The n. profundus (*n. pr*) runs together with the r. ophthalmicus lateralis (*r. o. lat*) through the profundus canal to the dorsal side of the ethmoidal region. After passing forwards there in the groove *gr. pr* it enters the nasal cavity through the opening in the tectum nasi situated at the anterior end of the groove, leaving the nasal cavity through the fenestra endonarina communis. It is worthy of notice that the n. profundus varies in its course in relation to the m. obliquus superior in that it passes sometimes above and sometimes below this muscle when entering the profundus canal (cf. Lehn 1918, p. 392; Allis 1922, p. 273). During its passage through the anterior part of the orbit the nerve gives off a branch which according to Lehn (1918, p. 392) goes to the skin above the eye after piercing the part of the supraorbital sensory canal enclosed in the frontal. In the ethmoidal region the nerve gives off two dorsal branches[1] both of which accompany branches of the r. ophthalmicus lateralis.

The r. maxillaris V and the r. buccalis lateralis form a truncus infraorbitalis (*r. mx + buc*). This truncus leaves the antero-latero-ventral corner of the orbit through the opening *ap. buc* (fig. 5 A), passing immediately laterally to a vertical ligament connecting the palatoquadrate with the lateral margin of the overlaying part of the endocranium (see Pollard 1892, pl. 30, fig. 33; Sewertzoff 1928, p. 310, figs. 52 E, 53 A). In its further course forward it is first situated in the groove *gr. buc* (fig. 5 B), thence entering the nasal cavity through the opening *f. buc* (figs. 5 B, 6 B, 7, 9). Within the nasal cavity it runs forwards, according to Lehn (1918, p. 385), in a groove along the ventral margin of the fenestra endonarina. After sending out a few small twigs through the fenestra endonarina it leaves the nasal cavity through a canal (*c. buct*, fig. 7) in its anterior wall.

During its passage in the orbit the r. palatinus VII divides into one lateral ($r. pal_l$, fig. 9) and one medial branch ($r. pal_m$). The lateral branch pierces the ectopterygoid (*Ecpt*), thence passing along the lateral edge of this bone. At a few places it anastomoses with the r. maxillaris V. The medial branch of the r. palatinus "passes beneath the nasal capsule, there lying at first in the tissues immediately mesial to the mesial dermopalatine (the so-called vomer), and then dorsal to the latter bone"[2] (Allis 1922, p. 281). According to Pollard (1892, p. 396) there is also another branch which enters the nasal cavity, where, judging from his figures (33, 34; pl. 30), it has its passage between the floor of the nasal cavity and the nasal sac.

The snout is said by Allis to receive its blood-supply through four arteries: the a. ophthalmica, the a. orbitonasalis, the a. maxillaris, and a branch of the a. cerebralis anterior. The a. ophthalmica (*a. o*, fig. 9) accompanies the n. profundus and the r. ophthalmicus lateralis. The a. orbitonasalis (*a. on*) gives off a few branches which accompany the r. palatinus. As has already been mentioned it pierces the interorbital wall through a canal of its own (*c. a. on*). Through this canal it reaches the canalis olfactorius in which, together with the olfactory nerve, it passes forwards to the nasal cavity, where in the nasal sac it anastomoses with a branch of the a. maxillaris. The latter artery

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[1] These three branches possibly belong to the r. frontalis (portio ophthalmici profundi). The main part of the nerve here described as the n. profundus is probably only the ventral profundus branch (r. ophthalmicus profundus or r. nasalis; cf. pp. 253—254 and Allis 1918).

[2] Regarding the "mesial dermopalatine" cf. below p. 608.

(*a. mx*), together with the truncus infraorbitalis, enters the nasal cavity through the foramen *f. buc.* It sends out a branch to the nasal sac, anastomosing with the a. orbitonasalis as just mentioned, then leaves the nasal cavity through the fenestra endonarina. The branch of the a. cerebralis anterior joins the olfactory nerve and enters the nasal cavity together with that nerve.

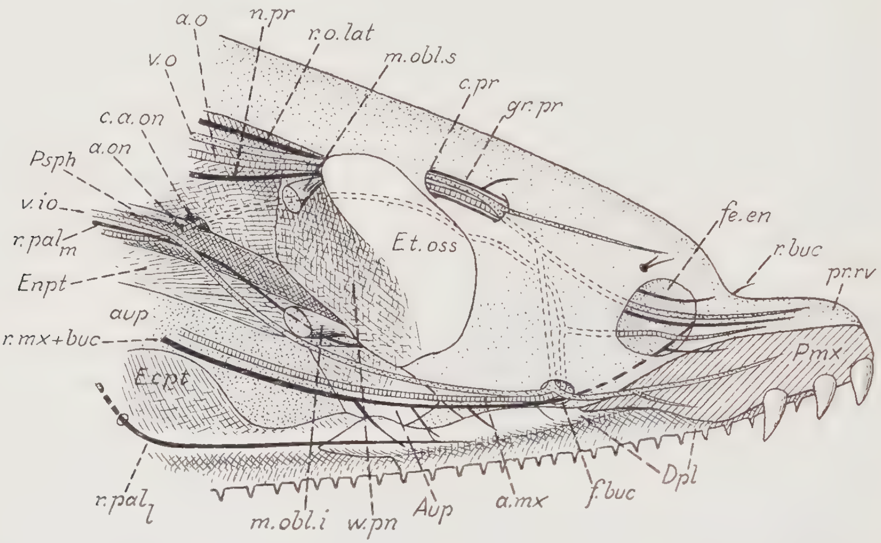

Fig. 9. *Polypterus bichir.* Diagram showing the course of the most important nerves and vessels of the snout in relation to the endocranium and palatoquadrate complex. Lateral view. Cartilage dotted. The cross-ruled area between parasphenoid and entopterygoid represents a ligament. $^9/_2$. Compilation after Allis (1922).

Aup, autopalatine; *Dpl,* dermopalatine; *Ecpt,* ectopterygoid; *Enpt,* entopterygoid; *Et. oss,* "ectethmoid"; *Pmx,* compound "premaxillary"; *Psph,* parasphenoid; *a. mx,* maxillary artery; *a. o,* ophthalmic artery; *a. on,* orbitonasal artery; *aup,* cartilaginous part of pars autopalatina; *c. a. on,* canal for orbitonasal artery; *c. pr,* profundus canal; *f. buc,* foramen for r. buccalis lateralis, r. maxillaris V, and vessels; *fe. en,* fenestra endonarina communis (fenestra endonarina anterior + posterior); *gr. pr,* groove for n. profundus, r. maxillaris V, and vessels; *m. obl. i, m. obl. s,* m. obliquus inferior and m. obliquus superior; *n. pr,* n. profundus; *pr. rv,* ventral rostral process; *r. buc,* r. buccalis lateralis; *r. mx + buc,* r. maxillaris V and r. buccalis lateralis (truncus infraorbitalis); *r. o. lat,* r. ophthalmicus lateralis; $r.pal_l$, $r.pal_m$, lateral and medial branches of r. palatinus VII; *v. io,* infraorbital vein; *v. o,* ophthalmic vein; *w. pn,* postnasal wall.

Besides by veins accompanying the r. palatinus VII the blood of the snout is collected also by two other veins, the v. ophthalmica, accompanying the a. ophthalmica, and the v. infraorbitalis. The v. ophthalmica (*v. o,* fig. 9) is formed by the confluence of one medial and one lateral branch. The medial branch goes backwards above the nasal capsule and receives the blood from the anterior and dorso-medial parts of the snout. The lateral branch drains the foremost lateral parts of the snout. It enters the nasal cavity by the fenestra endonarina and after passing backwards and upwards it leaves the nasal cavity through its roof, through the foramen at the anterior end of the groove *gr. pr.* In this groove it unites with the medial branch forming together with this the v. ophthalmica. After entering the orbit through the profundus canal the v. ophthalmica goes backwards in the dorsal part of the orbit where, according to ALLIS (1922, p. 261), it receives inter alia two dorsal branches which descend through the roof of the orbit, and two branches from the brain which separately pierce the cranial wall. No details of the foramina of the two last-mentioned veins are to be found in ALLIS' description (according to LEHN, 1918, fig. 3; cf. fig. 6 A above, *f. v*, there are two vein foramina in the dorsal part of the lateral wall of the cranial cavity in front of the trigeminus exit, the foremost of these foramina lying straight above the trochlearis foramen). Of the two branches from the brain mentioned by ALLIS, the anterior one according to VAN GELDEREN (1924, pp. 557, 558; 1925, pp. 584, 589) represents the v. cerebralis anterior while the posterior is by him called the v. media spuria. The v. infraorbitalis (*v. io*, fig. 9) which comes from the tip of the snout, goes backwards along the ventral margin of the lateral side of the ethmoidal region, receiving a considerable tributary from the nasal cavity through the foramen *f. buc.* This tributary anastomoses within the nasal sac with a branch of the v. ophthalmica and receives a vein from the brain through the canalis olfactorius.

With regard to the sensory canals and dermal bones of the snout of *Polypterus* see below p. 602 and fig. 84.

C. **Sturgeons, Amia, and other Actinopterygians.**

The ethmoidal region in sturgeons (fig. 10 A, B), *Amia* (fig. 10 C, D), and higher Actinopterygians (HOLMGREN and STENSIÖ 1936; DE BEER 1937) is of a much less complicated structure than the corresponding region in sharks and *Polypterus.* The nasal cavity (*cav. nc*, fig. 10) is generally a mere pit, the nasal pit, separated from its antimere by a nasal septum (*sn*). Roof, anterior wall and side-wall are generally entirely absent. In addition to the septum nasi, the solum nasi and the postnasal wall are its only boundaries. Through the canalis olfactorius (*c. olf*) which is frequently of some length, the nasal cavity is connected backwards with the cranial cavity. Exceptions to this rule are those forms in which the olfactory nerve passes through the anterior part of the orbit and in which the anterior part of the canalis olfactorius leads from the orbit to the nasal cavity.

In most Actinopterygians (PETER 1901; LIERMANN 1933; MATTHES 1934, pp. 888—892; REINKE 1936; LAIBACH 1937) the nasal sac is furnished with two external openings, one anterior and one posterior, separated by a bridge of soft tissue. The anterior nasal tube may often be much extended, whereas this is less common in the case of the posterior one. The mucous membrane of the nasal sac is generally strongly folded, the folds being arranged as a rosette. This arrangement is typical of Teleosts but is also found in *Acipenser* and *Amia.* It should be mentioned that in *Polypterus* the mucous membrane of the nasal sac is folded in a very different manner (cf. pp. 261—262 and figs. 7, 8). The nasal sac may enclose only a main cavity as in *Acipenser* and *Amia*, but may also, as in many Teleosts, be furnished with a number of diverticles which are frequently quite complicated. These diverticles may be strongly developed and in *Cynoglossus* the nasal sacs of both sides even have a common median diverticle which according to KYLE (1900) is in communication with the cavity of the mouth by a median unpaired opening. As pointed out by MATTHES (1934, p. 890) this communication between the cavity of the nasal sac and the mouth must not be mistaken for a choana, but should be regarded as a secondary formation.[1]

In the ethmoidal region in *Amia* there are two paired cartilage-bones, the ectethmoid (*Ece*) and the preethmoid (*Pe*, fig. 10 C, D). The preethmoid, a small ossification in the anterior part of the floor of the nasal cavity, has been homologized by BRIDGE (1877), ALLIS (1897, 1898), WEGNER (1922), and others, to the septomaxillary in Tetrapods. As will be demonstrated below (p. 402), the so-called septomaxillary in Urodeles, or the nariodal as it has been called here (see above, p. 249), is clearly a cartilage-bone, too, but as it is an ossification in the lateral nasal wall, behind the fenestra endonarina, it cannot possibly correspond to the preethmoid in *Amia.* The septomaxillary in Anurans and higher Tetrapods is a dermal bone and cannot, therefore, represent the preethmoid in *Amia.* WEGNER thus commits a serious mistake when in his attempts to explain the origin and homologues of the septomaxillary he starts from the preethmoid in *Amia.*

It would lead too far to deal in detail with the course of the nerves and vessels in the snout of the Actinopterygians. However, the following deserves mentioning.

The r. ophthalmicus lateralis is in *Amia* and in most other Actinopterygians closely connected with the n. profundus.

In sturgeons, however, it is independent. In *Acipenser* (STENSIÖ 1925, pp. 76—77, fig. 15; cf. NORRIS 1925, pls. 5—7) it goes from the orbit forwards and somewhat laterally to the upper face of the ethmoidal region at the postero-dorsal border of the nasal pit. In this part of its

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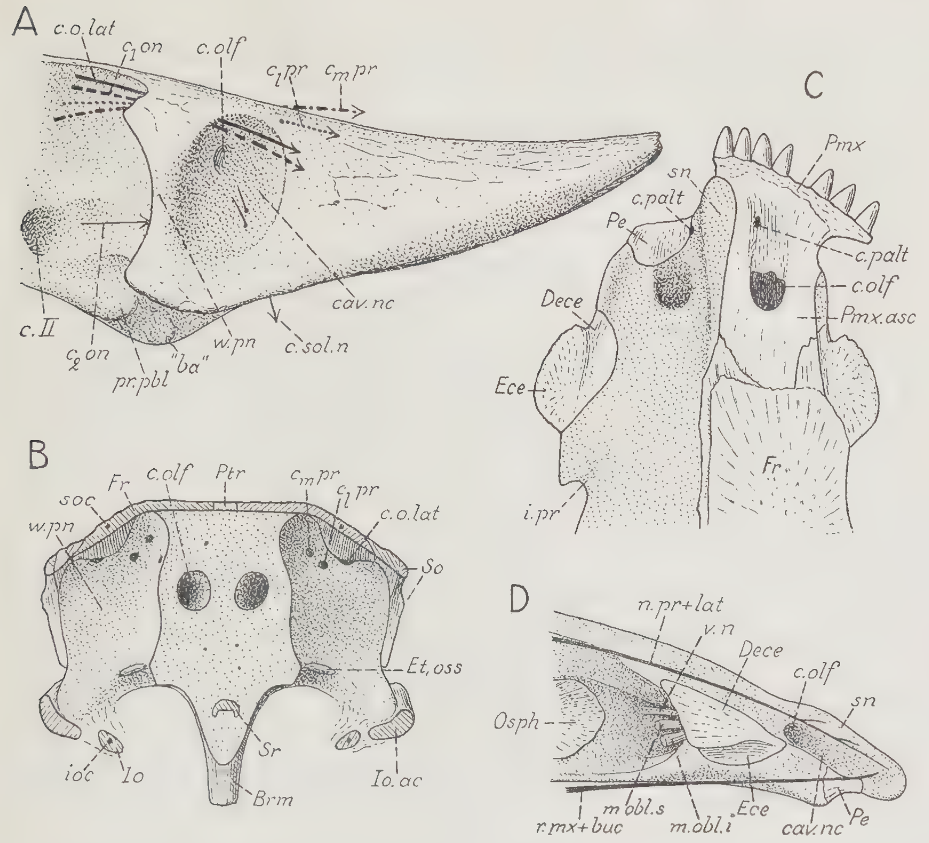
[1] According to JOHNSTONE (1904) the perforation in the roof of the mouth observed by KYLE is probably an artifact caused by a parasitic Copepod.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c.o.lat
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Fig. 10. *A*, *B*, *Acipenser sturio*. *A*, anterior parts of endocranium in lateral view. The course of several of the canals indicated by arrows. This figure drawn after the endocranium figured by STENSIÖ (1932, figs. 34 and 35). $^{3}/_{4}$. *B*, anterior part of endocranium with its dermal bones in posterior view. $^{3}/_{2}$. *C*, *D*, *Amia calva*. *C*, anterior parts of endocranium with the premaxillary and frontal of the right side in position. *D*, anterior parts of endocranium seen from the right side. Figures *C* and *D* compilations after ALLIS (1897, 1898). Cartilaginous parts of the endocranium denoted by dotting.

Brm, median basirostral; *Dece*, dermectethmoid; *Ece*, ectethmoid; *Et. oss*, perichondral bone lamina on the lower medial part of the posterior face of the postnasal wall (ectethmoid, W. K. PARKER 1882; HOLMGREN and STENSIÖ 1936; lateral ethmoid, DE BEER 1937); *Fr*, frontal; *Io*, infraorbital; *Io. ac*, accessory infraorbital; *Osph*, orbitosphenoid; *Pe*, preethmoid; *Pmx*, premaxillary; *Pmx. asc*, ascending process of premaxillary; *Ptr*, postrostral; *So*, supraorbital; *Sr*, subrostral; "*ba*", "basal angle"; *cav. nc*, cavity of nasal capsule; $c_l pr$, $c_m pr$, canals for lateral and medial terminal branches respectively of n. profundus; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. palt*, canal for terminal branch of r. palatinus VII; *c. sol. n*, canal piercing solum nasi; $c_1 on$, canal probably corresponding to the orbitonasal canal in the description given by HOLMGREN and STENSIÖ; $c_2 on$, narrow canal possibly corresponding to the orbitonasal canal of DE BEER's description; *c. II*, canal for optic nerve; *ioc*, infraorbital sensory canal; *i. pr*, notch for profundus nerve; *m. obl. i*, *m. obl. s*, m. obliquus inferior and m. obliquus superior resp.; *n. pr + lat*, n. profundus and r. ophthalmicus lateralis; *pr. pbl*, lateral palatobasal process of SEWERTZOFF's description, basipterygoid process of STENSIÖ's and DE BEER's descriptions; *r. mx + buc*, r. maxillaris V and r. buccalis lateralis; *sn*, septum nasi; *soc*, supraorbital sensory canal: *v. n*, nasal vein; *w. pn*, postnasal wall.

course it is either enclosed in a canal in the ethmoidal region (*c. o. lat*, fig. 10 A) or runs in a canal between the endocranium and the dermal bones (*c. o. lat*, fig. 10 B). From the postero-dorsal border of the nasal pit the nerve continues downwards and slightly forwards through the bridge of soft tissue separating the anterior and posterior nostrils. During the latter part of its course it passes close underneath the supraorbital sensory canal (cf. below, p. 346).

The n. profundus is strangely developed in Actinopterygians (Allis 1918; Norris 1925, pp. 350—362; Haller v. Hallerstein 1934, pp. 578—579). In Selachians (cf. pp. 253—254), *Polypterus* (Allis 1922, p. 272), Dipnoans (cf. foot-note 1 on p. 282 and Allis 1918, pp. 73, 74, 78), and Amphibians (cf. foot-note 1 on p. 302) its ventral branch (r. ophthalmicus profundus, r. nasalis or r. nasociliaris; cf. Goodrich 1930, p. 750) is most strongly developed, whereas in Actinopterygians the reverse condition is found. In the latter the ventral profundus branch is weak and does not reach the snout, while the dorsal branch, the r. frontalis (portio ophthalmici profundi), is strongly developed. The fibres of the dorsal branch are, however, intermingled with those of the r. ophthalmicus superficialis V. Judging by appearances the portio ophthalmici profundi and the r. ophthalmicus superficialis V thus form a common trunk in Actinopterygians. Since it is uncertain whether the fibres in this nerve that belong to the r. ophthalmicus superficialis V go so far forward as to participate in the innervation of the snout to any very great extent, I have here referred to the entire nerve as the n. profundus (cf. above p. 254).

In *Acipenser* (Kurz 1924, p. 55, fig. 8; Stensiö 1925, p. 77, fig. 15; Holmgren and Stensiö 1936, p. 435; De Beer 1937, p. 92) the n. profundus leaves the orbit through a canal, the profundus canal, which pierces the dorso-medial part of the postnasal wall and emerges on the upper face of the ethmoidal region medially to the nasal pit. On entering the posterior opening of the profundus canal the nerve in question runs medially to the origin of the m. obliquus superior (according to De Beer 1937, p. 92, the m. obliquus superior originates from the posterior aperture of the profundus canal). In two specimens of *Acipenser sturio* (figs. 10 A and 10 B) examined by me, the dorso-medial part of the postnasal wall is pierced by two canals (c_lpr, c_mpr) of about the same diameter. The position and course of these canals would appear to indicate that each gives passage to a large branch of the n. profundus. If this be true, the nerve probably even as far caudally as in the orbit bifurcates into two strong terminal branches just as occurs in *Scaphirhynchus* (Norris 1925, pl. 6). The two canals continue on the upper side of the ethmoidal region in the shape of deep grooves or canals running forwards and dividing into several branches. In *Amia* (ALLIS 1897, p. 598; pl. 23, figs. 19, 20; pl. 24, fig. 21; pl. 26, figs. 29, 30, *opt;* NORRIS 1925, pl. 1) the n. profundus, as mentioned above, accompanies the r. ophthalmicus lateralis, in appearance completely fused with it. The common nerve-trunk thus formed (*n. pr + lat*, fig. 10 D) leaves the orbit through a notch (*i. pr*, fig. 10 C) in the dorso-medial part of the upper edge of the post-nasal wall then going forwards on the upper side of the ethmoidal region medially to the two nostrils while giving off branches to the sensory-organs and the skin.

The so-called orbitonasal canal in *Amia* (ALLIS 1897, pp. 513—514, pl. 21, fig. 9, *onc;* pl. 25, fig. 25, *onfn;* HOLMGREN and STENSIÖ 1936, p. 453; DE BEER 1937, p. 101) connects the orbit with the canalis olfactorius. The two oblique eye muscles (*m. obl. i*, *m. obl. s*, fig. 10 D) extend inwards through the whole canal and have their origin at the nasal septum, this according to DE BEER. The canal is also traversed by a large vein (*v. n*, fig. 10 D; vena nasalis, HOLMGREN and STENSIÖ) from the nasal cavity. In sturgeons no corresponding canal seems to exist. According to HOLMGREN and STENSIÖ (1936, p. 435, fig. 334) the orbital vein in *Acipenser* enters "ventrokaudal von der oberen Ecke der Orbita" a canal which they call the "Orbitonasalkanal". However, they give no further details of either the canal or the vein. In one of the two *Acipenser* specimens I have examined (fig. 10 A) there is a narrow canal which may be identical with the vein canal observed by HOLMGREN and STENSIÖ. This narrow canal ($c_1 on$, fig. 10 A) comes from the nasal cavity and pierces the postnasal wall close to and almost parallel with the canal for the r. ophthalmicus lateralis (*c. o. lat*). DE BEER (1937, p. 93) described a vein in *Acipenser* passing from "the region beneath the nasal capsule" through a canal in the postnasal wall backwards to the orbit where it empties into the orbital sinus. The canal for this vein, by DE BEER called the "orbitonasal canal", may possibly be identified with a fine canal passing in a similar manner ($c_2 on$, fig. 10 A) and found in one of the two sturgeon crania examined by me. As regards the vein itself, it may possibly correspond to a vein in *Polyodon* mentioned by STENSIÖ (1925, p. 79) which leaves the posterior part of the nasal cavity in a fine canal directed backwards-downwards and the ventral opening of which is situated at the edge between the posterior and ventral faces of the ethmoidal region. On the other hand it is uncertain whether it corresponds to the orbital vein mentioned by HOLMGREN and STENSIÖ.

The palatoquadrate in sturgeons (SEWERTZOFF 1928, pp. 258—261, 308; HOLMGREN and STENSIÖ 1936; DE BEER 1937) is very short and does not extend beneath the ethmoidal region. It is unparalleled in Actinopterygians and Teleostomes altogether in that its anterior end meets the palatoquadrate of the other side in a median symphysis beneath the foremost part of the interorbital wall. By a ligament (*Scaphirhynchus*) or connective tissue only (*Acipenser*) it is suspended on a paired process, by SEWERTZOFF called the lateral palatobasal process (*pr. pbl*, fig. 10 A). This process, situated in the anterior part of the interorbital wall below, but mainly in front of the opticus foramen (*f. II*), has been interpreted by DE BEER (1925, pp. 677—679; 1937, p. 93; pl. 30, fig. 7; pl. 31, fig. 1, *btp;* see also STENSIÖ 1932, fig. 34; HOLMGREN and STENSIÖ 1936, p. 435, fig. 334) as a basipterygoid process. The palatoquadrate in sturgeons is thus devoid of a palatine process. This is by SEWERTZOFF regarded as a primitive but by STENSIÖ (1932, pp. 91—93) as a secondary condition. In *Amia* (see inter alia SEWERTZOFF 1928, figs. 32, 52 D; pl. 9, fig. 35) the processus palatinus articulates with the postero-ventro-lateral corner of the ethmoidal region.

D. **Dipnoi.**

The endoskeleton of the snout of recent Dipnoans (HUXLEY 1876; BRÜHL 1880; WIEDERSHEIM 1880; WINSLOW 1898; BRIDGE 1898; SEWERTZOFF 1902; FÜRBRINGER 1904; AGAR 1906; GOODRICH 1909, 1930; KRAWETZ 1911; GREIL 1913; KISSELEWA 1929; KESTEVEN 1931 a; HOLMGREN and STENSIÖ 1936; DE BEER 1937) consists of cartilage only. The ethmoidal region is very imperfect, being formed only of a median septum nasi, a paired lateral plate protruding from either lateral side of the septum nasi, and at least two cartilages on each side situated posterior and ventrally respectively to the nasal cavity. These cartilages are, as we shall see, the posterior one of the two postnasal cartilages, and the subnasal cartilage. Because of its imperfect development the ethmoidal region has usually no well defined canals for nerves and vessels.

The septum nasi, which is low, is in *Neoceratodus* (*sn*, figs. 11 A, 12 A) well developed throughout its extent, whereas in *Protopterus* (WINSLOW 1898, p. 189, pl. 4, fig. 32) and *Lepidosiren* (BRIDGE 1898, pl. 28, figs. 3, 4; pl. 29, figs, 11, 12) it is reduced in its posterior ventral parts (figs. 11 B, 12 B). The paired lateral plate (fig. 12) which is continuous only with the dorso-lateral border of the septum, is dome-shaped and perforated by foramina or fenestrae. It forms the whole tectum nasi, but extends as far downwards anteriorly, laterally and posteriorly as also to bound the nasal cavity antero-dorsally, latero-dorsally and postero-dorsally. The other parts of the nasal capsule are made up of connective tissue in which the postnasal cartilage or cartilages and the subnasal cartilage are embedded.

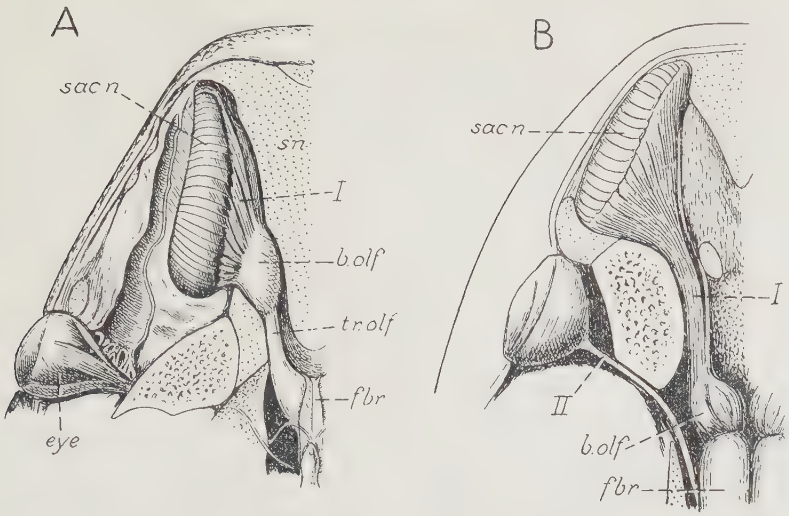

Fig. 11. Left half of the anterior part of the head in dorsal aspect. Dorsal parts removed so as to show the nasal sac, olfactory nerve and eye-bulb. *A*, of *Neoceratodus forsteri*. *B*, of *Protopterus annectens*. From Bing and Burckhardt (1905, figs. 1 and 20).

b. olf, bulbus olfactorius; *fbr*, forebrain; *sac n*, nasal sac; *sn*, septum nasi; *tr. olf*, tractus olfactorius; *I*, n. olfactorius; *II*, n. opticus.

The postnasal cartilage or cartilages are situated in the connective tissue between the nasal cavity and the orbit and topographically, therefore, they occupy a position corresponding somewhat to that of the middle and ventral parts of the postnasal wall. In *Neoceratodus* there is one, but in *Protopterus* and *Lepidosiren* two paired postnasal cartilages. The postnasal cartilage in *Neoceratodus* ("*pr. ao*", figs. 12 A, 14) is independent in the adult but arises, as demonstrated by Sewertzoff (1902, p. 602), as a process from the trabecula ventrally to the opticus exit. In embryonic stages it reminds of the "processus antorbitalis" (lamina orbitonasalis, cf. above, p. 243) in Urodeles and is therefore so termed by most scientists (Gaupp 1905, p. 685; Kravetz 1911; Greil 1913; De Beer 1937). Some workers however (Huxley 1876; Allis 1919, pp. 181—182) regard it as an upper labial cartilage, while it is called the "Ethmoidalfortsatz" by Sewertzoff (1902) and Holmgren and Stensiö (1936). Of the two postnasal cartilages in *Protopterus* and *Lepidosiren* (fig. 12 B) the posterior ("*pr. ao*") is the one strongest developed. This cartilage is continuous with the cranial wall ventrally to the opticus exit and bifurcates distally into two shanks. In the former respect it agrees with the so-called processus antorbitalis in the *Neoceratodus* larva and is for this reason usually considered homologous to that process (Agar 1906, p. 57) and generally called the processus antorbitalis. Close in front of the cartilage just treated lies the other, the anterior, of the two postnasal cartilages (*lab*). Whether this element should be regarded as a labial cartilage, as is the opinion of Huxley (1876), Bridge (1898), and Agar (1906), or whether, as maintained by Fürbringer (1904), it represents part of the nasal capsule, as does the posterior one (and its homologue in *Neoceratodus*), is a question that can be decided only by an embryological investigation.

The nasal cavity in Dipnoans lacks a true floor and has therefore a large ventral opening.

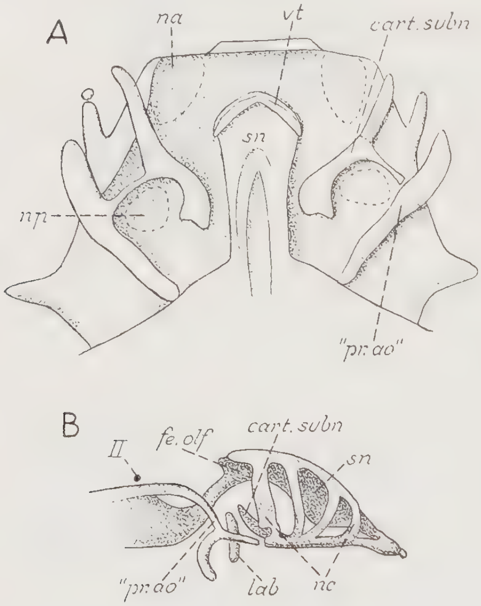

Fig. 12. *A, Neoceratodus forsteri.* Anterior part of endocranium with vomerine teeth. Ventral view. From Fürbringer (1904, pl. 39, fig. 27). The right side of the figure altered according to observations by Allis (1919, pp. 180—182). The position of the nostrils shown by broken lines. *B, Lepidosiren paradoxa.* Anterior part of endocranium in lateral view. Larva, stage 38. From Agar (1906, pl. 3, fig. 16).

cart. subn, subnasal cartilage; *fe. olf,* fenestra olfactoria; *lab,* anterior postnasal cartilage; *na,* incurrent nasal opening; *nc,* nasal capsule; *np,* excurrent nasal opening; "*pr. ao*", posterior postnasal cartilage ("processus antorbitalis"); *sn,* septum nasi; *vt,* vomerine tooth; *II,* n. opticus.

The subnasal cartilage (*cart. subn*, fig. 12; cf. fig. 13) lies in the connective tissue ventrally to the nasal cavity. In *Protopterus* and *Lepidosiren* it forms a simple skeletal bar, which from the ventral margin of the fenestrated lateral cartilaginous plate of the ethmoidal region issues in an almost postero-medial direction between the two nasal apertures and underneath the nasal sac. While in *Protopterus* (Winslow 1898, pp. 189—190; pl. 4, fig. 32) it ends free in the soft tissue beneath the nasal sac, it is in *Lepidosiren* (Bridge 1898, pp. 340—341) connected by a fibrous tissue with the ventral edge of the posterior part of the septum nasi. In *Neoceratodus* the cartilage in question has no connection either with the septum nasi or with the lateral paired plate of the ethmoidal region, but is an entirely independent skeletal element. As will be seen from fig. 12 A (*cart. subn*), where it is shown in ventral view, it is here of a more complicated structure than in *Protopterus* and *Lepidosiren.*

The subnasal cartilage was first observed and described by Huxley (1876) in *Neoceratodus*. As we have seen, in *Neoceratodus* it has no direct connection with the skeleton of the nasal capsule and it was partly for this reason that Huxley interpreted it as an anterior upper labial cartilage. Bridge (1898, pp. 340—341) established later on that the subnasal cartilage is developed also in *Lepidosiren*. However, on finding that in this genus it has a lateral connection with the cartilage of the ethmoidal region, he concluded that it must be a part of the nasal capsule and that in *Neoceratodus* it has been detached secondarily from that capsule. This conception of the nature of the subnasal cartilage was also adopted by Fürbringer (1904, p. 481). Agar (1906, p. 57), who discovered in *Lepidosiren* that the cartilage in question arises from an independent primordium, considered this to prove that it could not belong to the nasal capsule and like Huxley, he interpreted it as a labial cartilage. Allis (1919, p. 181), finally, arrived at the conclusion that the subnasal cartilage corresponds to the ala nasalis in Selachians (Allis 1919, pp. 163—164, 181). The reason why Allis came to this conclusion is that the ala nasalis in his opinion is an independent element, not part of the nasal capsule itself.

As is evident from the above, there are three different interpretations of the subnasal cartilage. Of these Bridge's and Fürbringer's is the most plausible. The fact that the subnasal cartilage arises embryologically as an independent element without any connection with the other parts of the nasal capsule can no longer be quoted against Bridge's and Fürbringer's interpretation, since it is now established (Gaupp 1905, p. 586; Hammarberg 1937, p. 264, fig. 38) that the skeleton of the nasal capsule may be formed from many different centres. As I will demonstrate in the following, there are many reasons definitely in favour of the opinion that the subnasal cartilage belongs to the nasal capsule. We shall also see that it even appears probable that the subnasal cartilage is actually part of the lateral wall of the nasal capsule or, more precisely, that part of the lateral nasal wall which separates the fenestra endonarina anterior from the fenestra endonarina posterior. In my opinion this part of the lateral nasal wall has shifted from a primarily lateral to a ventral position so as secondarily to be situated in the roof of the mouth.

The large ventral opening of the nasal cavity is divided by the subnasal cartilage into two divisions, an anterior one for the incurrent nostril and a posterior one for the excurrent nostril. By the majority of authors the excurrent nostril has hitherto been interpreted as a choana, homologous to that of the Tetrapods (Bawden 1894, p. 120; Peter 1901, p. 21; Wiedersheim 1909, p. 376; Plate 1924, pp. 304, 353; Sewertzoff 1926 a; Ihle, etc. 1927; Goodrich 1930, p. 248; Kesteven 1931, p. 184, Säve-Söderbergh 1934; Holmgren and Stensiö 1936, p. 386; Romer

1937; Broman 1939). Should this interpretation of the excurrent nostril as a choana be correct, the natural consequence would be (Gaupp 1905, p. 686) that the anterior and posterior divisions of the ventral opening of the nasal cavity must correspond to the fenestra endonarina anterior and the fenestra endochoanalis, respectively, in Tetrapods and other Choanate Vertebrates (Rhipidistid Crossopterygians). A logical sequence of this interpretation of the excurrent nostril would be to regard the subnasal cartilage as a structure strictly homologous to the lamina nariochoanalis which in Rhipidistid Crossopterygians (see pp. 441—442) and Amphibians separates the fenestra endonarina anterior from the fenestra endochoanalis (*la. nch*, figs. 1, 16, 22 A, C, 46 C, 47, 48).

That the excurrent nostril of Dipnoans is a true choana has for good reasons been doubted by Greil (1913, p. 1485) and Allis (1919; 1932; 1932 a, p. 666; 1935, p. 289; 1936, p. 313). In his investigations of the labial formations in fishes and Tetrapods the latter scientist arrived at the conclusion that the two nostrils of the Dipnoans correspond to the anterior and posterior nostrils of fishes in general, and that the posterior nostril of Dipnoans and other fishes represents the nasolachrymal duct of Tetrapods. Thus finding himself obliged to interpret the excurrent nostril of Dipnoans as a posterior external nostril, he arrives at the conclusion that the Dipnoans lack a true choana.

We shall now discuss the subnasal cartilage and the nostrils in Dipnoans in order to attain as far as possible a definite opinion of the homologues of these formations.

The subnasal cartilage in *Dipnoi* (*cart. subn*, figs. 12, 13 B) is so orientated that its longitudinal axis runs from the front laterally in a backward and medial direction. As we have seen, its antero-lateral end lies close below (*Neoceratodus*) or is directly connected with (*Protopterus*, *Lepidosiren*) the lower lateral part of the paired lateral fenestrated cartilaginous plate of the ethmoidal region, while its posterior end is close to (*Neoceratodus*, *Protopterus*) or joins the posterior part of the septum nasi (*Lepidosiren*). The lamina nariochoanalis in Rhipidistid Crossopterygians and Amphibians has an entirely different position (*la. nch*, figs. 13 A, 16, 17, 46, 47, 70 A). Its longitudinal axis goes from the front and medially in a direction backwards and laterally, thus having essentially another direction in relation to the longitudinal axis of the head than that of the subnasal cartilage. The lamina nariochoanalis constitutes an anterior part of the lateral nasal wall and usually also an adjoining lateral part of the ventral nasal wall (the solum nasi), thus participating in the formation of two of the walls of the nasal cavity.

The lamina nariochoanalis in Urodeles is formed during the embryonic development of a lateral process from the anterior part of the trabecula (cf. below on this p.). This process, the trabecular horn (cf. fig. 13 A, *trab. c*), grows out backwards between the external incurrent nostril (*na*) and the choana (*ch*). More precisely, morphologically postero-ventro-medially to the external incurrent nostril and antero-dorso-laterally to the choana. In Urodeles the incurrent nostril therefore lies morphologically dorso-laterally or antero-dorso-laterally to the lamina nariochoanalis and the choana ventro-medially or postero-ventro-medially to that lamina. In the embryonic stages a formation is found in Dipnoans (cf. fig. 13 B, "*trab. c*") that resembles the trabecular horn in Urodeles and is considered by De Beer (1937, pp. 171, 180, 395—396) to be homologous to the trabecular horn in Urodeles and Tetrapods in general. In the posterior (postero-medial) extension of this "trabecular horn" in the Dipnoans arises the primordium of the subnasal cartilage, which thus ostensibly is a posterior (postero-medial) prolongation of the "trabecular horn". The "trabecular horn" and the subnasal cartilage are formed dorso-laterally to the anterior incurrent nostril (*na*, fig. 13 B) and ventro-medially to the posterior excurrent nostril (*np*). The incurrent nostril thus lies ventro-medially and the excurrent nostril dorso-laterally to the "trabecular horn" and the subnasal cartilage. In their relations to the "trabecular horn" the nostrils in the Dipnoans thus have such a position that the anterior incurrent nostril would be comparable to the choana in Tetrapods in general while the posterior excurrent nostril would represent an external nostril.[1] Such an interpretation of the nostrils in Dipnoans is of course quite impossible, for there is no reason for assuming or even suspecting that the incurrent nostril in them should not be homologous to the external nostril in the Tetrapods. It is, therefore, quite obvious that the "trabecular horn" of the Dipnoans cannot be homologous to that of the Tetrapods (cf. Kesteven 1931 a, p. 243). This is also evident from their embryonic development of which a brief account must, therefore, be given here.

In larvae of Urodeles (Gaupp 1905, pp. 688—698; Stadtmüller 1924; 1936, pp. 519—521, 546; Chung 1932; De Beer 1937, pp. 177—180) the foremost part of the trabecula is round and rod-like. By the formation of cartilage on the lateral side of the trabecula close behind its tip a process grows out in a lateral direction from the anterior part of the trabecula. This is the trabecular horn (cf. fig. 13 A, *trab. c*). Simultaneously with the trabecular horn the trabecula forms also two other processes, one lateral and one dorsal. The lateral one, called the "processus antorbitalis" ("*pr. ao*"), arises behind the trabecular horn, whereas the dorsal process originates from the tissue dorsally to the anterior part of the trabecula. The latter process forms the medial wall of the nasal cavity. In the Dipnoans, however, we find entirely different conditions. In the early stages of development the trabeculae in them do not reach the ethmoidal region (SEWERTZOFF 1902, fig. 1; AGAR 1906, pl. 2, fig. 7). In later stages an unpaired cartilage is developed in the ethmoidal region of the Dipnoans, the ethmoid plate (DE BEER 1937, pp. 169, 174), which is connected posteriorly with the trabeculae and which, according to GREIL (1913, p. 1196), arises from an independent primordium. The ethmoidal plate develops into the nasal septum from the dorsal and anterior parts of which certain paired processes grow out in later stages. In *Neoceratodus* there are anteriorly formed two such processes, one postero-dorsal and one antero-ventral (KRAWETZ 1911, pl. 4, fig. 5). It is the latter of these two processes that DE BEER calls the "trabecular horn" and homologizes to the trabecular horn of the Tetrapods. As regards this process it would thus appear that it is not formed from the trabecula but from the foremost part of the nasal septum, thus having another and more dorsal origin than the trabecular horn in Tetrapods. Already in 1911 KRAWETZ stressed this fact (p. 343; cf. KESTEVEN 1931 a, p. 243; HOLMGREN and STENSIÖ 1936, p. 373) writing regarding this process: ". . . so zeigt die Entwickelungsgeschichte, dass wir es in ihnen nicht mit Vorsprüngen der freien Enden der Trabekeln, sondern mit der Vorderwand des Septum nasale zu tun haben . . .". In *Lepidosiren* (AGAR 1906, p. 57; cf. fig. 12 B above) four paired processes grow out from the dorsal edge of the nasal septum laterally and downwards to fuse with the ventral rim of the "basket-work" of the nasal capsule. This ventral rim of the "basket-work" arises later than the processes mentioned as a lateral outgrowth from the anterior end of the nasal septum. It is this outgrowth in *Lepidosiren* that has been called the "trabecular horn", but as seen from its embryonic development it is actually of a different origin than the trabecular horn of the Tetrapods.

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[1] It is true that De Beer (1937, pp. 395—396) looks upon the "trabecular horn" in Dipnoans and Tetrapods as homologous formations. He emphasizes, however, that the "trabecular horns" in Dipnoans and Tetrapods occupy different positions in relation to the nostrils, though without touching upon the consequence this must have in respect of the interpretations of the subnasal cartilage and the nostrils in Dipnoans.

As may be gathered from the above statements the so-called trabecular horn of the Dipnoans has not only another topographical position than the true trabecular horn of Tetrapods, but differs also from this in its embryonic development. It is evident, therefore, that it cannot possibly be a true trabecular horn. Judging from its position and from the position of the parts of the nasal capsule formed by it in adults, it is comparable to and in all probability the exact equivalent of the part of the nasal capsule in Urodeles that is situated just above the fenestra endonarina anterior (*fe. ena*, fig. 46 C; cf. fig. 13 A). The

Dipnoans are thus completely devoid of a true trabecular horn and in consequence also of a lamina nariochoanalis, which, as we have seen, is formed by the true trabecular horn. Under these conditions the subnasal cartilage cannot of course be a posterior continuation of a true trabecular horn. Its position and connection with the so-called trabecular horn shows that the subnasal cartilage must be interpreted as a postero-ventral prolongation of the skeletal mass above the incurrent nostril whence follows that its homologue in the Urodeles must probably be sought for in the part of the lateral wall of the nasal capsule lying between the fenestra endonarina anterior and the fenestra endonaria posterior (figs. 13 A, 46 B, C).[1] The fenestra endonarina posterior in Urodeles lets through the nasolachrymal duct, but this duct, as will be

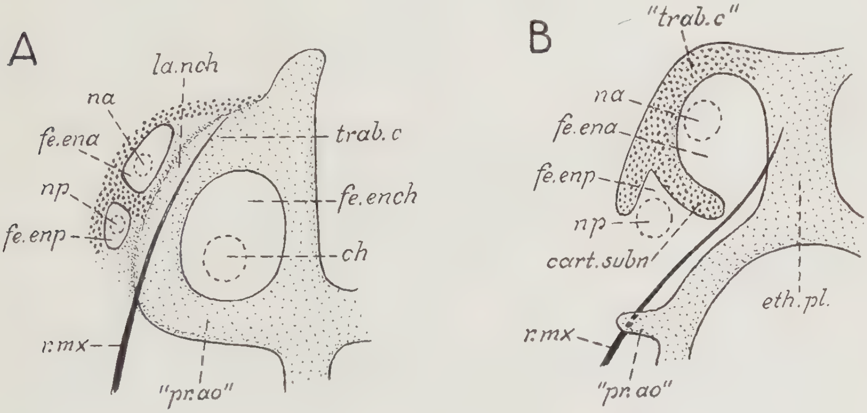

Fig. 13. Diagrams illustrating the position of the nasal openings in relation to the skeleton of the nasal capsule and to the r. maxillaris V. *A*, in a Choanate Gnathostome in general in ventro-lateral aspect; *B*, in a Dipnoan in ventral aspect. The coarsely dotted parts of the skeleton of the nasal capsules are regarded as homologous. That a true choana was primarily present in the ancestors of the *Dipnoi* and in the primitive *Dipnoi* seems very unlikely.

cart. subn, subnasal cartilage, homologous to the part of the lateral wall of the nasal capsule in other Gnathostomes, that separates the fenestra endonarina anterior and the fenestra endonarina posterior; *ch*, choana; *eth. pl*, ethmoid plate; *fe. ena*, fenestra endonarina anterior; *fe. ench*, fenestra endochoanalis; *fe. enp*, fenestra endonarina posterior; *la. nch*, lamina nariochoanalis; *na*, anterior external (or incurrent) nostril; *np*, posterior external (or excurrent) nostril; "*pr. ao*", in *A*, part of postnasal wall formed by "processus antorbitalis", in *B*, posterior postnasal cartilage ("process antorbitalis") in an initial stage of development; *r. mx*, r. maxillaris V; *trab. c*, part of the wall of the nasal cavity formed by the true trabecular horn; "*trab. c*", part of the wall of the nasal cavity (the ventral rim of the anterior part of the "basket-work") formed by the so-called trabecular horn.

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[1] In Rhipidistid Crossopterygians (figs. 40, 47—49) the part of the lateral nasal wall separating the fenestrae endonarinae anterior and posterior is much more strongly developed than in the Urodeles, in which it may sometimes be absent (see pp. 287—289).

seen below (p. 402), has its exact homologue in the posterior external nasal tube in *Porolepiformes* and other fishes, and it would thus appear that the excurrent nostril in Dipnoans is a posterior external nostril.

The opinion that the excurrent nostril in Dipnoans is no choana but a posterior external nasal opening is also borne out by the following facts.

1) In early embryonic stages the olfactory organ in Dipnoans has one opening only, as in other Gnathostomes. When this primary external opening is later divided into one incurrent and one excurrent nostril this occurs in the same manner as when the anterior and posterior external nostrils are separated from each other in non-choanate fishes (Semon 1893, p. 44; 1901, p. 6; Kerr 1909, p. 4; Allis 1932, p. 652; Matthes 1934, p. 892; Reinke 1936, p. 618).

2) The r. maxillaris (*r. mx*, fig. 13) in *Neoceratodus* (cf. p. 281 below) runs far forwards into the ethmoidal region as it did or does in the majority of fishes (figs. 2, 4, 9, 10 D, 59—61, 78 B) and Tetrapods (cf. pp. 304, 329—330, figs. 29, 30). In *Neoceratodus* (*r. mx*, fig. 14), this nerve passes medially to the excurrent nostril. In those of the vertebrates with a true choana in which it has a corresponding forward extent into the ethmoidal region it always passes within and above the pons nariochoanalis, that is the bridge of tissues separating the choana from the external nostril, formed inter alia also by the lamina nariochoanalis. In these choanate vertebrates the nerve in question thus runs mainly ventrally to the external nostrils and laterally or dorso-laterally to the choana. Accordingly we find that in its position in relation to the r. maxillaris V the excurrent nostril in Dipnoans or at least in *Neoceratodus* does not resemble a choana but an external nostril.

3) In Dipnoans or in any case in *Neoceratodus* the bridge of tissues that separates the incurrent and excurrent nostrils and which includes inter alia also the subnasal cartilage is not pierced by any very large vessels. In this respect this bridge therefore does not resemble a true pons nariochoanalis, but agrees most closely with the mass of tissues that separates the anterior and posterior external nostrils in other fishes and Tetrapods (cf. figs. 2—4, 9, 29, 30, 59, 61, 78 B).

4) In early larval stages the primary undivided nostril of the Dipnoans is situated in front of and somewhat laterally to the mouth opening and thus entirely outside the mouth cavity (Kerr 1910, pp. 495—499, fig. 6 A, B). Pretty soon, however, it migrates backwards and downwards. In this way it acquires such a position that, as is well known, the excurrent nostril opens in the roof of the mouth cavity in a way similar to that of the choana in choanate vertebrates, whereas the incurrent nostril lies in the foremost part of the mouth cavity, at the very

labial edge of the mouth. The migration in question, which seems to take place simultaneously with the subdivision of the primary nostril into an incurrent anterior and an excurrent posterior nostril, shows clearly that the strange ventral position of the nostrils in Dipnoans must be a secondary one. The incurrent and excurrent nostrils in Dipnoans were thus primarily external nasal apertures which both lay on the dorsal side of the snout (WATSON 1926, p. 198; ALLIS 1936, p. 305). Despite the transformations that have taken place in the nasal capsule in connection with the postero-ventral shifting of the nostrils to the mouth, the r. maxillaris V has retained its primary position ventrally to the two nostrils.

5) The infraorbital sensory canal in Dipnoans (KINGSBURY 1895 a; GOODRICH 1930, figs. 721—724; HILLS 1933; ALLIS 1934, p. 367; HOLMGREN and STENSIÖ 1936, fig. 291; FORSTER-COOPER 1937, fig. 6; HOLMGREN 1942, pp. 27—29) ends anteriorly about opposite the incurrent nostril. It therefore forms no ethmoidal commissure and thus does not communicate with its fellow of the opposite side at the tip of the snout as in fishes in general. This condition is undoubtedly due to the transformations occurring in the snout in connection with the shifting of the external nostrils backwards and downwards into the mouth (ALLIS 1936, p. 305). The mass of tissue ventrally to the external nostrils that normally in fishes forms the anterior ventro-lateral part of the snout has become bent downwards and inwards by the shifting of the nostrils so as to form part of the roof of the mouth cavity. The ethmoidal part of the infraorbital sensory canal primarily passing through the said mass of tissues was, therefore, pushed inwards into the mouth, and consequently became of no use and got lost.

An interesting feature in this connection is that a secondary shifting of the nostrils in a ventral direction towards the mouth opening has taken place also in sharks (cf. also regarding Ichthyostegids below, p. 622). In primitive sharks, e. g. *Chlamydoselachus* (fig. 2), both nostrils are situated on the lateral side of the snout whereas in the majority of forms they are found on the ventral side of the snout. For instance in *Cestracion* (HUXLEY 1876 a, p. 25) and *Heterodontus* (ALLIS 1919, pl. 2, figs. 6, 7; DANIEL 1934, p. 264) the excurrent nostril may be so near the edge of the mouth that the flow of water enters the cavity of the mouth on its way from the olfactory organ. The migration of the nostrils in sharks downwards towards the mouth opening, which is traceable during the embryological development (see MATTHES 1934, p. 886), has caused a displacement of the infraorbital sensory canal in an oral direction, but also in *Heterodontus* this sensory canal encircles the oral edge of the excurrent aperture (ALLIS 1919, p. 159). A further migration of the nostrils towards or into the cavity of the mouth would certainly, as has happened in the Dipnoans, lead to a reduction of the part of the infraorbital sensory canal situated orally to the excurrent nostril.

6) The olfactory organ of Dipnoans has no respiratory function, but is exclusively a sensory organ (KERR 1910, p. 597; 1932, p. 423; BROMAN 1939 a). Neither the respiratory water nor the respiratory air passes through it. It has thus a far more one-sided function than the corresponding organ in Amphibians (cf. GOODRICH 1930, p. 597; WERNER 1930—1931, fig. 103).

It is evident from what has been stated that the subnasal cartilage represents that part of the nasal capsule which in Crossopterygians and certain Urodeles separates the fenestra endonarina anterior from the fenestra endonarina posterior.

Thus it may be considered fully established that the incurrent and excurrent nostrils in Dipnoans are anterior and posterior external nostrils respectively which have migrated down to the roof of the mouth cavity. This migration of the two external nostrils together with the coalescence of the teeth into large plates has caused great secondary changes in the structure of the nasal capsule and the entire ethmoidal region. If a true choana was primarily present it may very well have become lost during these considerable changes of the mouth. There are, however, no facts either anatomic or ontogenetic that speak in favour of such an assumption and the absence of a true choana is therefore most probably a primary condition.

The nasal sac of the Dipnoans (*sac n*, figs. 11 A, B, 14) is oblong or rather ovoid (MATTHES 1934; BROMAN 1939). In its dorsal and lateral parts it is provided with strong transversal folds connected by irregular weaker longitudinal folds, but folds are absent in the ventral part. From the latter part the incurrent and excurrent nostrils, which have been shown to be the anterior and posterior external nostrils, lead down to the mouth cavity (cf. HUXLEY 1876 a). In larvae of *Protopterus* and *Lepidosiren* (KERR 1909; FULLARTON 1933; BROMAN 1939) the posterior part of the nasal sac has a lateral diverticle which does not persist in the adults. In *Neoceratodus* this diverticle appears to be absent also in the larvae (BROMAN). Owing to its position in relation to the excurrent nostril it has been considered by KERR and BROMAN to represent the so-called Jacobson organ in Urodeles. This interpretation which is mainly based on the earlier conception of the excurrent nostril as a true choana is henceforth untenable, however, since the excurrent nostril has actually turned out to be a posterior external nostril (cf. p. 391).

In *Neoceratodus* (figs. 11 A, 14; HOLMGREN and van der HORST 1925) the olfactory nerve (*I*) is short while the bulbus olfactorius (*b. olf*) is elongate and separated from the high forebrain (*fbr*) by a likewise elongate tractus olfactorius (*tr. olf*). In *Protopterus* (fig. 11 B; BURCKHARDT 1892; WIEDERSHEIM 1909, figs. 201—202; PLATE 1922, fig. 515) and *Lepidosiren* (KERR 1902, pl. 26, figs. 8, 9; pl. 27, fig. 10), however, the olfactory nerve is long, but the bulbus olfactorius short and situated close to the forebrain.

We shall now deal with the other nerves of the snout, turning first to *Neoceratodus*. The works hitherto published (BEAUREGARD 1881; van WIJHE 1882; SANDERS 1889; SEWERTZOFF 1902; GREIL 1913) on this form contain but few or incomplete data. From the figures and plates in GREIL's (1913) large work it is possible with some difficulty to gather the following particulars concerning the course of the nerves in *Neoceratodus* in its larval development (fig. 14).

The r. ophthalmicus superficialis (*r. o. lat*) runs in connective tissue dorsally to the nasal sac and can be traced forwards to the tip of the snout. According to SEWERTZOFF (1902, p. 607) the trigeminus portion is very weak so that the nerve as a whole may properly be called a r. ophthalmicus lateralis. The n. profundus (*n. pr*) goes forwards high above the basal part of the posterior postnasal cartilage (the so-called antorbital process) and in the orbit it gives off a ventral branch which descends immediately behind the n. opticus. The destination of this ventral branch is not known. The nerve then continues forwards close above the dorsal face of the nasal sac laterally to the fila olfactoria where it gives off a dorsal branch and a little later a ventral or lateral branch which passes down along the outer side of the nasal sac. Above the anterior part of the nasal sac the nerve divides into two terminal branches which continue forwards down either side of the nasal sac. The r. maxillaris V (*r. mx*) goes close above the medial part of the postnasal cartilage, anastomosing just in front of that cartilage with the r. palatinus VII and then continuing forwards in the roof of the mouth ventrally to the medial part of the nasal sac. As already demonstrated by v. WIJHE (1882, p. 301) and as pointed out above (p. 278) it runs medially to the two nostrils (cf. *Lepidosiren*, BRIDGE 1898, p. 347).[1] The r. buccalis lateralis (*r. buc*) does not join the r. maxillaris V in the snout, as is otherwise mostly the case in fishes, but forms an entirely independent nerve. It goes forward in the upper lip quite far ventro-laterally to the nasal sac and the two nostrils. The r. palatinus VII (*r. pal*) runs, after anastomosing with the r. maxillaris

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[1] According to SANDERS (1889, p. 165) the r. maxillaris V bifurcates anteriorly into two branches which break up into numerous twigs for the upper lip.

V, ventrally to the septum nasi, but nothing is definitely known of its course (in the adult it seems to be partly enclosed in a canal in the ethmoidal region; cf. Holmgren and Stensiö 1936, p. 374).

In *Protopterus* (fig. 15; Humphry 1872; Pinkus 1895) the nerves in the snout run as follows (Pinkus).

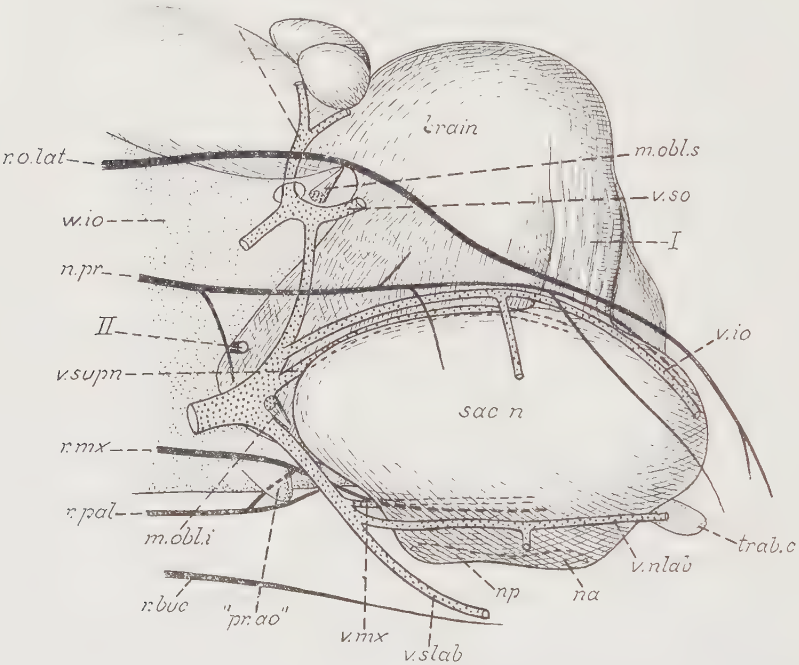

Fig. 14. *Neoceratodus forsteri.* Diagram of the nerves and veins in the anterior part of the head of a larva (Semon's stage 47) in their relation to the skeleton, brain and nasal sac. Lateral view. Compilation after Greil (1913, mainly pl. 54, fig. 2).

m. obl. i, m. obl. s, m. obliquus inferior and m. obliquus superior; *na, np,* incurrent and excurrent nasal openings; *n. pr,* n. profundus; "*pr. ao*", posterior postnasal cartilage ("processus antorbitalis") in an initial stage of development; *r. buc,* r. buccalis lateralis; *r. mx,* r. maxillaris V; *r. o. lat,* r. ophthalmicus lateralis; *r. pal,* r. palatinus VII; *sac n,* nasal sac; *trab. c,* "trabecular horn" in an initial stage of development; *v. ca,* v. cerebralis anterior; *v. io,* v. infraorbitalis; *v. mx,* v. maxillaris; *v. nlab,* v. nasolabialis; *v. slab,* v. supralabialis; *v. so,* v. supraorbitalis; *v. supn,* v. supranasalis; *w. io,* interorbital wall; *I,* n. olfactorius; *II,* n. opticus.

The r. ophthalmicus lateralis (*r. o. lat*) enters the nasal cavity through one of the fissures in the "basket-work" of the nasal capsule, leaving through the fissure next in front. The n. profundus (*n. pr*) is a strong nerve. Far back in the orbit it gives off two dorsal branches[1] of which the posterior goes to the skin above the eye and the anterior, partly accompanying the r. ophthalmicus lateralis, to the skin of the dorsal parts of the snout. Behind the eye the n. profundus divides into two main branches, one dorsal and one ventral. The former branch anastomoses with the r. maxillaris V and then enters the nasal cavity. After running a fairly long distance through that cavity, it leaves through one of the anterior fissures in its roof. The ventral main branch accompanies the r. buccalis lateralis (*r. buc*) forwards ventrally to the nasal capsule. After the anastomosis with the n. profundus, the r. maxillaris V (*r. mx*) runs in a forward direction to the upper lip. The courses of the ventral main branch of the n. profundus and of the r. buccalis lateralis and r. maxillaris V are not quite clear as regards their relation to the nostrils.

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[1] These branches probably represent the r. frontalis (portio ophthalmici profundi), while the remaining part of the nerve is the r. ophthalmicus profundus (Allis 1918, pp. 73—74; cf. above p. 254).

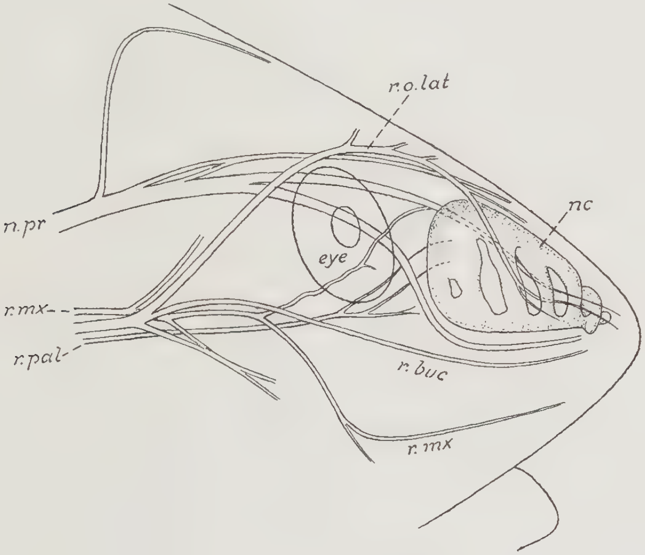


Fig. 15. *Protopterus annectens.* Diagram of the nerves in the snout. Lateral view. Compilation after PINKUS (1895).

nc, nasal capsule; *n. pr,* n. profundus; *r. buc,* r. buccalis lateralis; *r. mx,* r. maxillaris V; *r. o. lat,* r. ophthalmicus lateralis; *r. pal,* palatinus VII.

Our knowledge of the vessels in the snout of the Dipnoans (W. N. PARKER 1892; SPENCER 1893; KELLICOTT 1905) is incomplete. Above all this applies to the arteries, about which practically nothing can be said at present. GREIL has made a study of the veins in larvae of *Neoceratodus.* Judging from his figures the snout of the *Neoceratodus* larva in SEMON's stages 47 and 48 is drained by at least six veins (fig. 14). Two of these, the v. infraorbitalis and the v. supranasalis, run backwards along the upper face of the nasal sac on either side of the fila olfactoria (*v. io, v. supn*; GREIL 1913, pl. 53, fig. 3; pl. 54, fig. 2), while a third, the v. maxillaris (*v. mx*; visible only in a cross section of stage 48: Greil 1913, fig. 525, p. 1379), accompanies the r. maxillaris V backwards to the lower anterior part of the orbit. A fourth vein, the v. nasolabialis (*v. nlab*; Greil 1913, pl. 53, fig. 1; pl. 54, fig. 2), goes backwards ventro-laterally to the nasal sac, joining a fifth vein beneath the posterior part of the nasal sac, the v. supralabialis (*v. slab*; Greil 1913 pl. 54, fig. 2; fig. 525), which comes from the upper lip and accompanies the r. buccalis lateralis. The sixth vein (*v. so*, visible in Greil's figs. 1 and 3, pl. 53; in fig. 1 it is called the vena cerebralis anterior) passes from the upper side of the snout backwards to the upper antero-medial corner of the orbit, immediately below the m. obliquus superior. It may properly be called the vena supraorbitalis. An anastomosis connects this vein with the v. infraorbitalis (fig. 14) or possibly with the v. supranasalis. The v. cerebralis anterior (*v. ca*) leaves the cranial cavity through a foramen in the lateral wall just behind the origin of the m. obliquus superior, emptying in the v. supraorbitalis almost immediately after entering the orbit.

E. **Urodela, with special reference to Salamandra.**

The subsequent account of the Urodeles is based mainly on *Salamandra salamandra (maculosa)*. This species is one of the best known representatives of Urodeles. Its whole anatomy has been treated at some length by Francis (1934), whereas the embryological development of its skeleton has been described in detail by Stadtmüller (1924, 1936).

Descriptions of the skeleton and anatomy in general of the head or snout of Urodeles have been published by Hoffmann (1873—1878), Wiedersheim (1875, 1877, 1879), Born (1876), W. K. Parker (1877, 1882 a, 1882 b), H. H. Wilder (1891, 1892, 1903), Riese (1892), Seydel (1895), Osawa (1902), Terry (1906), Okajima (1906, 1908, 1909), Anton (1908, 1912), Noble (1921, 1931), Dolivo-Dobrovolsky (1926), Bolkay (1928), Chung (1929, 1931), Chung and Yatabe (1931), Herre (1933, 1935, 1939, 1941), Stadtmüller (1936), and others. The embryonic development of the skeleton of the snout has been dealt with by among others Winslow (1898), Gaupp (1905), Peeters (1910), Higgins (1920), Grote (1926), Aoyama (1927, 1930), Chung (1932), Kawagoe (1932), Erdmann (1933), Suzuki (1933), Stadtmüller (1936), Okutomi (1936), Fukuchi and Sisido (1936), De Beer (1937), Kudo (1938), Oomi (1938), and Bourque (1940).

The ethmoidal region in the metamorphosed *Salamandra* consists of cartilage only. In several other Urodeles, however, it has a small cartilage-bone, the nariodal (*Nd*, figs. 18 A, B, 46 B, C; cf. p. 249 above), which is situated at the postero-ventral corner of the fenestra endonarina communis. This cartilage-bone previously erroneously considered a septomaxillary (narial), will be dealt with below (pp. 293—295).

As in Selachians, the nasal cavities in *Salamandra* are widely separated from each other. The internasal wall is therefore broad. In this wall of the salamander we find 1) anteriorly a large unpaired cavity, the cavum internasale, which opens ventrally, and 2) posteriorly the anterior or ethmoidal part of the cranial cavity, which is completely separated from the cavum internasale.

As the corresponding cavity in other Urodeles, the cavum internasale in the salamander (*cav. in*, fig. 16 B; cf. also figs. 17, 18, 46 C) is an unpaired space opening ventrally and housing the intermaxillary gland. It is bounded laterally on either side by the anterior parts of the medial wall of the nasal cavity, and posteriorly, from the cranial cavity, by the lamina precerebralis (*la. prec*, fig. 16 C). Its dorsal boundary, which is incomplete anteriorly, is formed by the tectum internasale (*te. in*, fig. 16 A, B, D) and by a median unpaired process, the processus prenasalis superior medius (*pr. psm*, figs. 16 A, B, 20) projecting forwards from the tectum internasale. Ventrally, where its large opening is situated, the cavity has no endocranial boundary. The processus prenasalis superior medius is comparatively narrow in *Salamandra* and so long that its anterior part, which is slightly bent downwards, extends forwards into the divisio prenasalis communis, where it forms the antero-dorsal boundary of the median part of the cavum prenasale (see p. 287).

In certain Urodeles, e. g. *Triturus* (*Triton;* Gaupp 1905, figs. 351, 352), the lamina precerebralis is absent and thus the cavum internasale communicates with the cranial cavity by an opening, the fenestra precerebralis. It is of interest in this connection that the lamina precerebralis in *Salamandra* does not arise until in late embryonic stages. In early embryonic stages of *Salamandra* the brain projects through an opening (*fe. prec*, fig. 16 D), representing the fenestra precerebralis, far forwards into the ethmoidal region, occupying at least the posterior dorsal parts of the space that later on develops into the cavum internasale (cf. p. 396).

The processus prenasalis superior medius is developed in several Urodeles and has been differently interpreted (cf. Stadtmüller 1936, p. 562). In primitive Urodeles such as *Onychodactylus*, *Geomolge*, and *Pseudosalamandra* (Chung 1931; Stadtmüller 1936, pp. 561—562) in which the tectum internasale extends further forwards and is more complete than in *Salamandra* and in which it forms a complete or almost complete roof also of the anterior part of the cavum internasale, the process in question is short and broad and situated mainly or entirely in the divisio prenasalis communis (cf. fig. 46 B, *pr.psm*). On account of its development in the said primitive forms, the process is in all probability, as maintained by STADTMÜLLER (1936, p. 562), to be considered simply a remainder of a primarily fairly complete roof of the cavum internasale and the cavum prenasale (see pp. 398—400).

In *Amphiuma*, *Cryptobranchus*, *Menopoma*, and *Megalobatrachus* (WIEDERSHEIM 1877, pp. 396, 399—400; pl. 19, fig. 9; pl. 22, figs. 52, 53; HAY 1890, pp. 17, 20, 27; ANTON 1908, pp. 467—468; pl. 10, figs. 5—7; AOYAMA 1930, pp. 131, 159, figs. 15, 19; KUDO 1930, 1938, pp. 13, 73; KAWAGOE 1932, p. 714) there is a median unpaired independent cartilage referred to by AOYOMA as the cartilago infranasalis (*cart.inf*, fig. 46 B). This cartilage which is higher than broad and oval in transverse sections, divides the cavum internasale and cavum prenasale incompletely into right and left halves. It descends downwards somewhat below the level of the ventral opening of the cavum internasale, forming a median rostro-caudal ridge in the anterior part of the roof of the mouth. As will be shown below (p. 397) the cartilago infranasalis is to be considered a part of the internasal wall that has become secondarily independent.

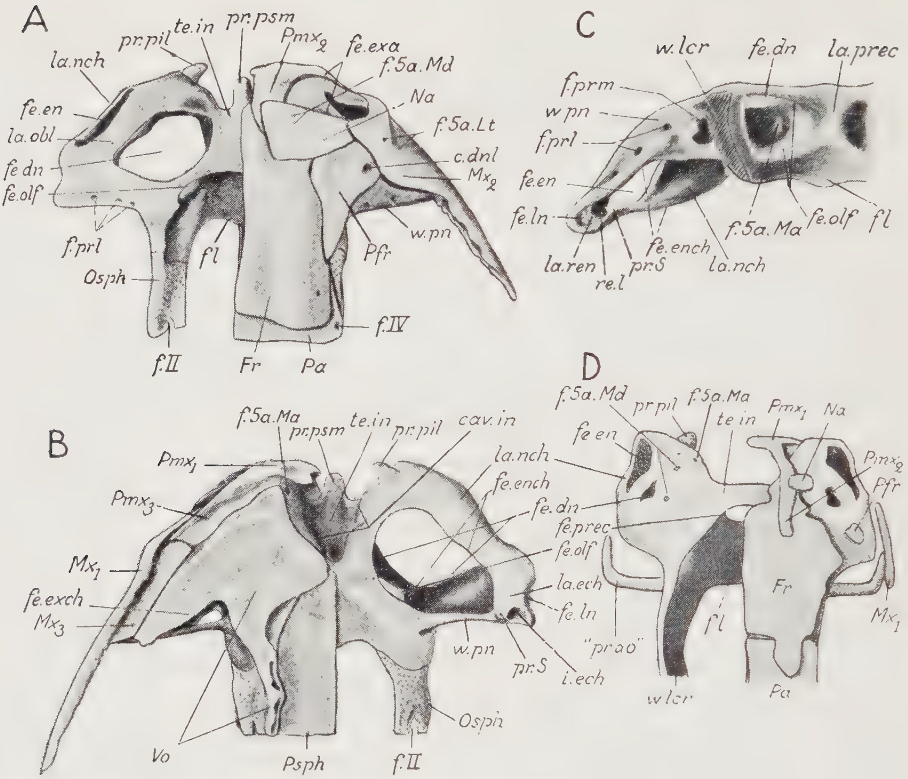
According to ALLIS (cf. p. 251 above; cf. also STADTMÜLLER 1936, p. 561) the cavum internasale of Urodeles is homologous to the cavum precerebrale of Selachians. These two cavities agree in that they are unpaired and situated in the internasal wall and that they are in communication posteriorly with the cranial cavity by a fenestra precerebralis. In other respects, however, they differ considerably from each other. The cavum precerebrale (*cav.prec*, fig. 3) is situated between the dorsal parts of the nasal capsules and is provided with a well developed floor, the internasal lamina (*la.in*), but is completely devoid of a roof. It is thus a cavity closed below, but open dorsally and in front. The cavum internasale, on the other hand, is developed throughout the whole depth of the ethmoidal region and has a roof, but no floor. It is thus a cavity opening downwards. As they differ considerably in their position and relations otherwise, the two cavities cannot of course be considered strictly homologous structures (see further p. 382 below).

In *Salamandra* and in other Urodeles as well, we find a paired process, the processus prenasalis inferior lateralis (*pr.pil*, figs. 16 A, B, D, 20; cf. also figs. 17, 46 B, C), which protrudes in a medio-anterior direction from the anterior ventral part of the medial wall of the nasal cavity. This process forms a support for the ventral portion of the pars facialis of the "premaxillary" (Pmx_2, fig. 16 A, D). Its posterior part traverses the antero-ventro-lateral corner of the cavum internasale and therefore belongs to the internasal wall; its foremost part, on the other hand, extends slightly in front of the transverse plane through the anterior ends of the nasal cavities and together with the foremost part of the processus prenasalis superior medius it is thus situated in the part of the ethmoidal region referred to in this work (cf. p. 245 above) as the divisio prenasalis communis. This division of the ethmoidal region which has only a slight rostro-caudal extent is occupied by a fairly small cavity continuous posteriorly with the cavum internasale, into which it passes over without any definite boundary. The said small cavity is traversed by the foremost part of the processus prenasalis inferior lateralis. It is bounded dorsally in its median and antero-median parts by the processus prenasalis superior medius, antero-laterally by the pars facialis (Pmx_2, fig. 16 A, D) of the "premaxillary", postero-laterally by the prenasal walls of either side, and ventrally by the antero-medial portion of the pars palatina (Pmx_3, fig. 16 B) of the "premaxillary". Being thus situated in the divisio prenasalis communis of the ethmoidal region, the small cavity in question should not be termed simply the anterior part of the cavum internasale, but must have a special name. As its essential characters resemble those of the cavum prenasale of the *Anura*, it will here be termed the cavum prenasale. It should be emphasized, however, that in all probability it has arisen independently of the similarly termed cavity of the *Anura* (cf. pp. 398—400, 489, 502).

The ethmoidal part of the cranial cavity in *Salamandra* is fairly short. It is bounded anteriorly by the lamina precerebralis, antero-laterally by the posterior part of the medial wall of the nasal cavity, and laterally by the postnasal wall. It is also provided with a floor (*fl*, fig. 16) and, in its anterior part, with a roof formed by the hinder part of the tectum internasale. The wall separating the cranial cavity from each nasal cavity is perforated by a wide fenestra olfactoria (*fe. olf*, fig. 16 A—C).

The walls of the nasal cavity in *Salamandra* are pierced by the fenestra olfactoria already mentioned and by four additional wide openings, the fenestra endonarina, the fenestra lateralis nasi, the fenestra dorsalis nasi, and the fenestra endochoanalis.

The fenestra endonarina (*fe. en*, figs. 16 A, 20; cf. also fig. 17 A) is situated in the anterior part of the lateral wall of the nasal cavity. As it gives passage to both the anterior external nasal tube and the posterior external nasal tube or nasolachrymal duct (cf. p. 402 below), it is a fenestra endonarina communis. In the Urodeles that possess a nariodal bone, which is a cartilage-bone developed in the lateral wall of the nasal cavity, the posterior external nasal tube or nasolachrymal duct leaves the nasal cavity through an opening of its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Pmx_2
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c.dnl
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Mx_2
fe.olf
w.pn
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fe.exch
fe.ln
Mx_3
w.pn
pr.S
i.ech
Osph
Vo
Psph
f.II
D
f.5a.Md
pr.pil
f.5a.Ma
te.in
Pmx_1
Na
fe.en
Pmx_2
Pfr
fe.dn
fe.prec
fe.olf
la.ech
Fr
fl
Mx_1
"pr.ao"
w.lcr
Pa

Fig. 16. *Salamandra salamandra* (*maculosa*). Skeleton of the snout. Dermal bones of left side removed to show the endocranium. *A—C*. Metamorphosed stage, 82 mm. After STADTMÜLLER (1924, figs. 22, 23 and 26). About $^7/_1$. *D*. Larva, 35 mm. After STADTMÜLLER (1924, fig. 1). About $^{14}/_1$. *A*, *D*, in dorsal and, *B*, in ventral aspects. *C*, left half in posterior view.

Fr, "frontal"; Mx_1, Mx_2, Mx_3, pars dentalis, pars facialis and pars palatina, resp., of maxillary; *Na*, "nasal"; *Osph*, orbitosphenoid; *Pa*, parietal; *Pfr*, prefrontal; Pmx_1, Pmx_2, Pmx_3, pars dentalis, pars facialis and pars palatina, resp., of "premaxillary"; *Psph*, parasphenoid; *Vo*, vomer; *cav. in*, cavum internasale; *c. dnl*, canal for ductus nasolacrimalis; *fe. dn*, fenestra dorsalis nasi; *fe. en*, fenestra endonarina communis (anterior + posterior); *fe. ench*, fenestra endochoanalis; *fe. ln*, fenestra lateralis nasi (fenestra infraconchalis); *fe. olf*, fenestra olfactoria; *fe. prec*, fenestra precerebralis; *fl*, floor of ethmoidal part of cranial cavity; *f. prl*, *f. prm*, lateral and medial profundus foramina; *f. 5 a. Lt*, foramen for a terminal twig of the lateral terminal branch of n. profundus; *f. 5 a. Ma*, *f. 5 a. Md*, foramina for anterior and dorsal twigs of the medial terminal branch of n. profundus; *f. II*, foramen for n. opticus; *f. IV*, foramen for n. trochlearis; *i. ech*, incisura ectochoanalis; *la. ech*, lamina ectochoanalis; *la. nch*, lamina nariochoanalis; *la. obl*, lamina obliqua; *la. prec*, lamina precerebralis; *la. ren*, lamina retronarina; "*pr. ao*", lamina orbitonasalis ("processus antorbitalis"); *pr. pil*, processus prenasalis inferior lateralis; *pr. psm*, processus prenasalis superior medius; *pr. S*, Seydel's palatal process ("Gaumenfortsatz"); *re. l*, recessus lateralis of cavity of nasal capsule; *te. in*, tectum internasale; *w. lcr*, lateral wall of cranial cavity; *w. pn*, postnasal wall.

own, a fenestra endonarina posterior (cf. fig. 46 B, C, *fe. enp*), and in these Urodeles the fenestrae endonarinae anterior and posterior are thus separated from each other. The fenestra endonarina posterior is there mostly situated immediately behind the nariodal bone between that and the posterior cartilaginous part (the lamina retronarina) of the lateral wall of the nasal cavity, but may also, as in *Plethodon* (Lapage 1928, p. 451) and *Spelerpes* (Stadtmüller 1936, p. 549), be developed in the said cartilaginous part of the lateral nasal wall somewhat behind the nariodal bone. The opening in the exoskeleton outside the fenestra endonarina communis is both in *Salamandra* and other Urodeles traversed by the anterior external nasal tube only, and is thus a fenestra exonarina anterior (*fe. exa,* fig. 16 A). The fenestra exonarina posterior is in *Salamandra* and Urodeles in general transformed into a long nasolachrymal canal which may be situated either in the lachrymal or in the prefrontal (*Salamandra*, *c. dnl*, fig. 16 A; cf. pp. 407—409).

The fenestra lateralis nasi (*fe. ln*, figs. 16 B, C, 20; cf. fig. 17) lies behind the fenestra endonarina communis from which it is separated by a bridge of cartilage, the lamina retronarina (*la. ren*, figs. 16 C, 20; cf. also fig. 17). This opening is developed for a lateral bulge (the ventral division of the lateral diverticle) of the nasal sac. In certain forms, e. g. *Geomolge*, *Hynobius nebulosus* (Chung 1931, p. 380), it is entirely absent.

The fenestra dorsalis nasi (*fe. dn*, figs. 16, 20; cf. also fig. 17) is an opening in the roof of the nasal cavity and is separated from the fenestra endonarina communis (the fenestra endonarina anterior and the fenestra endonarina posterior) by a bridge of cartilage, the lamina obliqua (*la. obl*, figs. 16 A, 20; cf. figs. 17 B, 18). It is closed by a membrane of connective tissue pierced by foramina for nerves and vessels ascending from the nasal cavity. In this connection it is of particular interest that in *Salamandra* the roof of the nasal cavity is more complete during its embryonic development than in the adult animals (fig. 16 D; Higgins 1920, pl. 2, fig. 13; Stadtmüller 1924, pp. 179—181). The fenestra dorsalis nasi is small in the salamander larva and the cartilage medially to it is there pierced by foramina for nerves and vessels. During the further development of the larva the fenestra dorsalis nasi increases in width, however, by the disappearance of the cartilage around it, finally fusing with the small foramina referred to, which were originally situated medially to it. The chondrification of the tectum nasi of *Salamandra* thus undergoes a regressive development during later embryonic stages. Also in other Urodeles, e. g. *Triturus* (*Molge*, Peeters 1910, pp. 63, 218), *Ambystoma* (fig. 17), and *Hynobius* (Chung 1932, pp. 348—349), the tectum nasi has been found to be more complete in the larvae than in the adult. As has been pointed out by HIGGINS (1920, pp. 14, 60—61) and others, the nasal capsule of the Urodeles reaches a maximum stage which is followed by a partial reduction of the cartilage formed.

The fenestra endochoanalis (*fe. ench*, figs. 16 B, 20; cf. figs. 17 B, 18) in *Salamandra* as well as in other Urodeles is an opening in the floor of the nasal cavity. It is very much larger than the fenestra exochoanalis (*fe. exch*, fig. 16 B), which is found underneath its posterior, medial part. The fenestra endochoanalis is bounded from the fenestra endonarina communis (the fenestra endonarina anterior and the fenestra endonarina posterior) by the lamina nariochoanalis (*la. nch*, figs. 16 A, B, 20; cf. figs. 17 B, 18; processus ventralis, WINSLOW 1898; Cartilago infranarina, STADTMÜLLER 1924; 1936, p. 548; CHUNG 1931). This lamina consists of two divisions, an upper vertical one which is the lower part of the lateral wall of the nasal cavity ventrally to the fenestra endonarina communis (the fenestra endonarina anterior and the fenestra endonarina posterior) and a lower horizontal one which constitutes the lateral part of the floor of the nasal cavity and forms the anterior and lateral boundary of the fenestra endochoanalis. The lamina nariochoanalis is continuous posteriorly with the lamina ectochoanalis (*la. ech*, figs. 16 B, 20) which separates the fenestra endochoanalis from

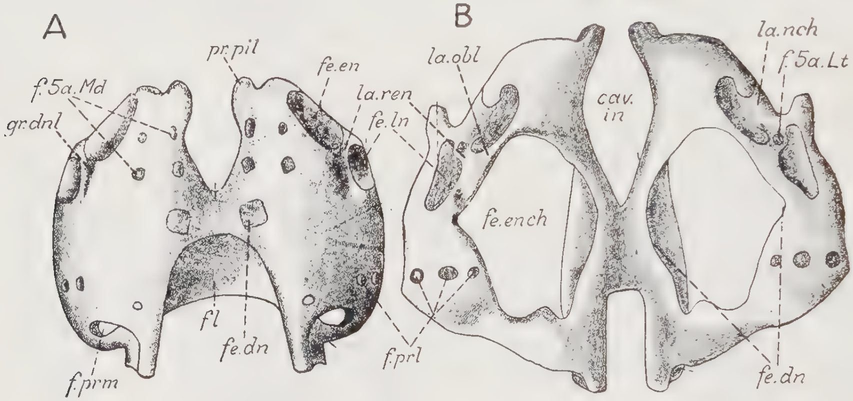

Fig. 17. *Ambystoma* (*Amblystoma*) *punctatum*. Anterior part of endocranium in dorsal view. *A*, larva, 55 mm, *B*, larva at the end of metamorphosis. From HIGGINS (1920, pl. 2, figs. 9 and 10).

cav. in, cavum internasale; *fe. dn*, fenestra dorsalis nasi; *fe. en*, fenestra endonarina communis; *fe. ench*, fenestra endochoanalis; *fe. ln*, fenestra lateralis nasi; *fl*, floor of most anterior part of cranial cavity; *f. prl*, *f. prm*, lateral and medial profundus foramen; *f. 5a. Lt*, foramen for terminal twig of lateral terminal branch of n. profundus; *f. 5a. Md*, foramen for dorsal terminal twig of medial terminal branch of n. profundus; *gr. dnl*, external nasolachrymal groove; *la. nch*, lamina nariochoanalis; *la. obl*, lamina obliqua; *la. ren*, lamina retronarina; *pr. pil*, processus prenasalis inferior lateralis.

the fenestra lateralis. The lower horizontal division of the latter lamina is produced backwards as a short process, ventrally to and beyond the posterior ventro-lateral corner of the postnasal wall. This short process, known as Seydel's palatal process (Seydel's "Gaumenfortsatz", *pr. S*, fig. 16 B, C), is separated from the postero-ventral corner of the lateral nasal wall by an incisure, the incisura ectochoanalis (*i. ech*, fig. 16 B; cf. fig. 46 B, C). The incisura ectochoanalis is in certain forms (*Hynobius tsushimensis*, *H. leechii*, *Pseudosalamandra*, CHUNG 1931, p. 379) continuous with the fenestra lateralis.

The postnasal wall (*w. pn*, fig. 16 A—C) in *Salamandra* which is almost transversal in position, is in its upper medial part pierced by a wide foramen, the medial profundus foramen (*f. prm*, figs. 16 C, 20), for the medial nasal branch (medial terminal branch) of the n. profundus. Laterally to this foramen there are two or three smaller foramina, the lateral profundus foramina (*f. prl*, figs. 16 A, C, 20; cf. fig. 17), which transmit lateral branches of the n. profundus and vessels.

As will be further shown below the medial nasal (medial terminal) branch of the n. profundus breaks up into a number of fine twigs most of which, at least in the majority of the Urodeles (*Salamandra*, figs. 16 D, 20, 21; *Ambystoma*, fig. 17 A; *Siredon*, GROTE 1926, pp. 472—473, figs. 1, 4, 5; *Cryptobranchus* (*Menopoma*), *Amphiuma*, H. H. WILDER 1892, pl. 12, fig. 1; pl. 13, fig. 6; *Diemictylus*, HIGGINS 1920, pl. 3, fig. 15), leave the nasal cavity through small foramina (*f. 5a. Ma*, *f. 5a. Md*) in the medial part of the tectum nasi and in the adjacent parts of the anterior and medial walls of the nasal cavity. The most anterior one of these foramina, which at least in certain forms gives passage to a fairly large twig, is usually referred to as the foramen apicale (cf. p. 244 above). According to FRANCIS (1934, p. 23) the foramen apicale is in *Salamandra* represented by a small foramen (*f. 5a. Ma*, fig. 16 B) ventrally to the base of the processus prenasalis inferior lateralis, a foramen which can only have transmitted a fairly fine nerve-twig. STADTMÜLLER (1924, fig 1), on the other hand, interpretes in *Salamandra* as the foramen apicale, a foramen (*f. 5a. Ma*, fig. 16 D) situated postero-dorso-medially to the base of the processus prenasalis inferior lateralis. These two writers have thus in *Salamandra* applied the term of foramen apicale to foramina which cannot possibly be identical and which seem to have given passage to different twigs of the highly ramifying medial nasal branch of the n. profundus. CHUNG (1931) points out that the "foramen apicale" is fairly variable in its position in the Japanese forms studied by him. In *Desmognathus* (I. W. WILDER 1913, fig. 19) a thick twig of the medial nasal branch of the n. profundus emerges from the nasal cavity through a fairly wide foramen in the medial nasal wall, a foramen which leads to the cavum internasale. The exits from the nasal cavity of the twigs of the medial nasal branch of the n. profundus thus appear to be so variable that a foramen apicale homologous in the various forms of Urodeles cannot be distinguished. We are therefore not justified in denominating in Urodeles any special anterior one of the foramina in question as the foramen apicale.

The nasal cavity consists in *Salamandra* and the majority of other Urodeles of a main chamber and a lateral recess (*re. l*, figs. 16 C, 18 C) forming the postero-ventro-lateral part of the cavity and situated laterally to the choana and ventrally and posteriorly to the fenestra endonarina (Born 1876, p. 626; Wiedersheim 1877, p. 480; 1909, fig. 246; cf. fig. 254 A—D; Riese 1892, pl. 9, fig. 4; pl. 10, fig. 9; Bawden 1894, pl. 5, fig. 8, Seydel 1895, figs. 10 D—G, 12 E—K; v. Mihalkovics 1898, pl. 1, figs. 1, 2; Bruner 1901, pl. 17, figs. 1—6; Higgins 1920, pl. 7, figs. 46—48; pl. 8, figs. 55, 62; Matthes 1927, fig. 4 b—h). In contradistinction to what is the case in *Anura*, the anterior and antero-lateral parts of the nasal cavity show no signs of a subdivision into compartments or recesses (cf. pp. 312—313).

The lateral recess of the nasal cavity houses the ventral division of the diverticulum laterale or the so-called Jacobson organ (see p. 301 below). It extends from somewhere ventrally to the fenestra endonarina communis or from ventrally to the posterior margin of the fenestra endonarina anterior backwards as far as to the posterior end of the nasal cavity. In the majority of forms it is only fairly slightly bounded off from the main chamber with which it is continuous anteriorly, and, except in *Ambystoma* (cf. p. 293 below), also medially. Posteriorly it opens into the mouth cavity just dorsally to Seydel's palatal process between that and the postero-ventro-lateral corner of the postnasal wall (see fig. 16 C). Its lateral and ventral boundaries are formed by the lamina ectochoanalis (*la. ech*), whereas its dorsal or dorso-medial (*Ambystoma*) boundary is a rostro-caudal crest. This crest, the crista rostrocaudalis (*ri. w. al*, fig. 18 B, C; cf. fig. 46 B, C; "concha nasalis" Wiedersheim; "turbinal prominence" Bruner; "Bindegewebswulst" Born), which is developed on the part of the lateral nasal wall that is situated dorsally to the fenestra lateralis nasi and behind the lamina obliqua (the "planum conchale"; Gaupp 1905, p. 699; Stadtmüller 1924, fig. 25; 1936, p. 547) forms the support of a fold of soft tissue, the plica rostro-caudalis, protruding into the nasal sac between its main cavity and lateral diverticle and partly also separating the dorsal and ventral divisions of the lateral diverticle from one another (see p. 301 below). The crest in question begins anteriorly close below the fenestra endonarina communis, thence extending backwards throughout the posterior part of the nasal cavity. It consists mostly of cartilage, or, where the nariodal bone participates in its formation, of bone and cartilage, but in certain forms, such as *Triturus* (Born 1876, p. 626; Matthes 1927, fig. 4 b—h) and *Tylotriton* (Riese 1892, p. 122), it is represented only by the connective tissue in the basal (lateral) part of the plica rostrocaudalis. Generally, for instance in *Salamandra*, it is not very prominent. However, in certain forms, e. g. *Plethodon* (fig. 18 C; Higgins 1920, pl. 8, fig. 62) and *Desmognathus* (Bruner 1901, pl. 17, fig. 5), it extends far medially into the nasal cavity, so that the lateral recess is very distinctly bounded off from the main chamber. In *Ambystoma* (fig. 18 B), where the nariodal bone participates in its formation, the crest is even so strongly developed as to extend ventro-medially to and fuse with the floor of the nasal cavity. By this excessive development of the rostrocaudal crest the lateral recess of the nasal cavity and the lateral diverticle of the nasal sac are in *Ambystoma* completely divided off medially from the other parts of the nasal cavity and nasal sac respectively.

On the outside of the lateral wall of the nasal cavity about opposite the crista rostro-caudalis and thus on the outside of the "planum conchale" (cf. Gaupp 1905, p. 699) there is a more or less marked logitudinal groove (*gr. dnl*, fig. 17 A; cf. Born 1876, pl. 39, fig. 6; Seydel 1895, fig. 10 E—F; Chung 1931, pl. 11 figs. 1, 3, 5, 7, 9, 11; pl. 12, figs. 13, 15, 17, 19). This groove ("impressio conchalis", Gaupp 1905, p. 701; Stadtmüller 1924, p. 185; Chung 1931), which leads backwards from the fenestra endonarina communis or fenestra endonarina posterior, is caused by the external part of the nasolachrymal duct, but besides that part of the nasolachrymal duct it houses also tubes of the glandula nasalis externa. It will here be referred to as the external nasolachrymal groove.

The crista rostro-caudalis and the external nasolachrymal groove have been suspected by previous writers to be a turbinal folding in an initial stage of development (see Wiedersheim 1877, p. 480; Born 1879, p. 136; Bawden 1894, p. 129; Seydel 1895, pp. 533—538; Gaupp 1905, p. 701; De Beer 1937, pp. 180, 397). The former of these two structures has, therefore, hitherto been known as the "concha nasalis" or "turbinal prominence", whereas the latter has previously been described as the "impressio conchalis". For reasons to be set forth below (pp. 406—407) it is highly conceivable, however, that these two structures are special formations without homologues in higher *Tetrapoda.*

In Urodeles with separate anterior and posterior endonarial fenestrae (thus not in *Salamandra* and other forms with a fenestra endonarina communis) there is between these two openings a small ossification, in this work termed the nariodal or nariodal bone (cf. p. 249 above).

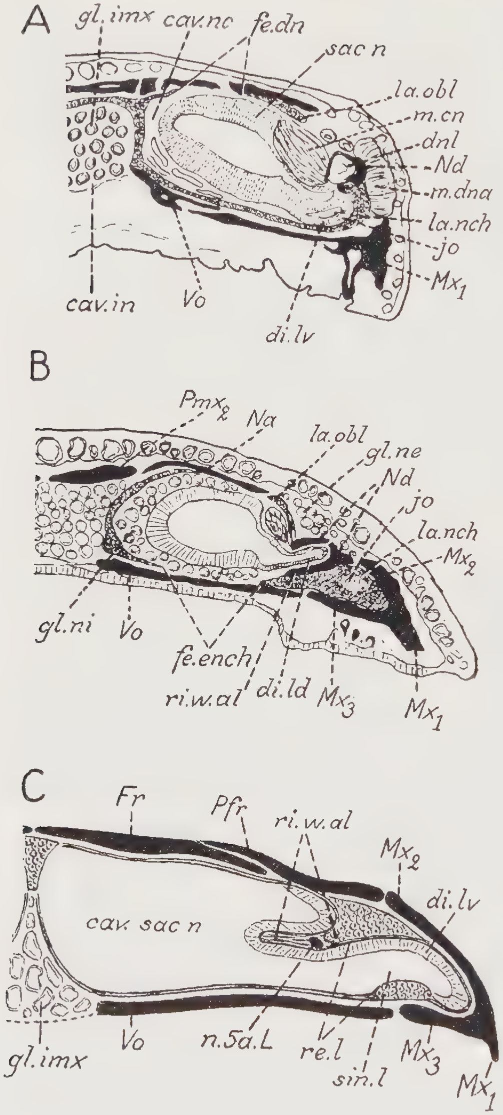
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Fig. 18. Transverse sections through the right half of the snout in certain Urodeles. *A*, and *B*, through the nariodal. *C*, through the posterior part of the nasal capsule. *A*, *Hynobius leechii.* $^{22}/_{1}$. *B*, *Ambystoma* (*Amblystoma*) *maculatum.* $^{12}/_{1}$. From Lapage (1928, pl. 7, fig. 18 and pl. 1, fig. 3). *C*, *Plethodon glutinosus.* From Wiedersheim (1877, pl. 24, fig. 81).

Fr, "frontal"; Mx_1, Mx_2, Mx_3, pars dentalis, pars facialis and pars palatina of maxillary; *Na*, "nasal"; *Nd*, nariodal; *Pfr*, prefrontal; Pmx_2, pars facialis of "premaxillary"; *Vo*, vomer; *cav. in*, cavum internasale; *cav. nc*, cavity of nasal capsule; *cav. sac n*, cavity of nasal sac; *dnl*, ductus nasolacrimalis; *di. ld*, *di. lv*, dorsal (anterior) and ventral (posterior) division of lateral diverticle of nasal sac; *fe. dn*, fenestra dorsalis nasi; *fe. ench*, fenestra endochoanalis; *gl. imx*, glandula intermaxillaris; *gl. ne*, *gl. ni*, glandula nasalis externa and interna; *jo*, Jacobson's organ; *la. nch*, lamina nariochoanalis; *la. obl*, lamina obliqua; *m. cn*, musculus constrictor naris; *m. dna*, musculus dilatator naris acessorius; *n. 5a. L*, lateral terminal branch of n. profundus; *re. l*, recessus lateralis of cavity of nasal capsule, *ri. w. al*, crista rostro-caudalis and plica rostro-caudalis; *sac n*, nasal sac; *sin. l*, sinus lateralis nasi.

The fact that this osssification is a cartilage-bone and not a dermal bone has recently been demonstrated by Lapage (1928) and Chung (1929; cf. also I. W. Wilder 1925) and this has been further corroborated by the investigations carried out for this work (cf. p. 402 below).

The nariodal (*Nd*, fig. 18 A, B; cf. fig. 46 B, C; Bruner 1901; Noble 1921; Lapage 1928; Chung 1929; Tsusaki and Chung 1929; Stadtmüller 1936) is always a small bone. In the majority of forms it extends from the fenestra endonarina anterior backwards to the fenestra endonarina posterior (fig. 46 C) and in these forms, in which it thus constitutes at least part of the anterior boundary of the fenestra endonarina posterior, it may be notched for the nasolachrymal duct posteriorly. In certain forms, e. g. *Plethodon* and *Spelerpes* (cf. p. 289 above), it ends already in front of the fenestra endonarina posterior, which is then bounded entirely by cartilage, as has already been pointed out (cf. fig. 46 B, *fe. enp*). The general development of the bone exhibits a wide range of variations in the various forms. It is simplest in such forms as *Plethodon*, *Desmognathus*, *Eurycea*, and *Hemidactylium*, where it has a laminar shape and seems to be entirely lateral to the intranasal part of the nasolachrymal duct. In *Ambystoma* (Bruner 1901, p. 321; pl. 17, fig. 6; Lapage 1928, pp. 447—448; pl. 1, figs. 2, 3), *Rhyacotriton* (Noble 1921, pl. 2, fig. 1), *Geomolge*, *Hynobius lichenatus*, and *H. leechii* (Chung 1929, p. 88), on the other hand, it is clearly influenced in its development by the said part of the nasolachrymal duct, being distinctly grooved in a rostro-caudal direction on its medial side so as to be gutter-shaped (*Nd*, fig. 18). The rostro-caudal groove, the internal nasolachrymal groove, thus found on the medial side of the bone in these forms houses not only the intranasal part of the ductus nasolacrimalis, but in addition most anteriorly also the part of the nasal sac (*di. ld*, fig. 19 B) from which issues the nasolachrymal duct. The groove is bounded ventrally by a pronounced crest which forms the foremost part of the crista rostro-caudalis already described (pp. 292—293). Finally, in certain forms, such as *Onychodactylus*, *Hynobius nebulosus*, and *H. tsushimensis* (Chung 1929, p. 89; according to Lapage also *H. leechii*), the nariodal is tube-shaped so as to completely surround the intranasal part of the nasolachrymal duct.

As is obvious from the above, the nasolachrymal duct in several of the forms with a nariodal bone passes backwards to the fenestra endonarina posterior either in a rostro-caudal groove on the medial side of the nariodal bone (figs. 18 A, B, 46 B, C; cf. fig. 46 A, *gr. ntp*) or through a rostro-caudal canal in that bone. After traversing the fenestra endonarina posterior the duct continues backwards on the outside of the nasal capsule. It then runs first in the external nasolachrymal groove (*gr. dnl*) thence further caudally entering a canal (*c. dnl*, figs. 16 A, 46 C) in the exoskeleton.

The palatoquadrate has been found in the larvae of several Urodeles to extend forwards to the ethmoidal region and to be connected with that region anteriorly, whereas in adult Urodeles it is practically always reduced anteriorly so as to end behind and not to be connected with the ethmoidal region. An exception is met with in *Ranodon*, however, where the palatoquadrate persists throughout its anterior extent and is connected with the ethmoidal region also in the adults.

The connections of the palatoquadrate with the ethmoidal region in larval stages and in the adult *Ranodon* are still very obscure.

According to EDGEWORTH (1925, pp. 227—234) the palatoquadrate in Urodeles has two different connections with the ethmoidal region: 1) a medial larval one with the "inner end" of the lamina orbitonasalis ("the processus antorbitalis") or with the trabecula just behind the lamina orbitonasalis, which is met with in larvae only, and 2) a lateral definitive one, with the ventro-lateral part of the postnasal wall, present only in adults. The medial larval connection ("vordere suspensorio-trabekuläre Verbindung", STADTMÜLLER 1936, p. 568), which has been found in many Urodeles (*Hynobius*, *Ranodon*, *Cryptobranchus*, *Megalobatrachus*, *Ambystoma*, *Desmoganthus*, *Spelerpes* and *Salamandrella*; HIGGINS 1920; EDGEWORTH 1923, 1925; AOYAMA 1930; cf. STADTMÜLLER 1936, p. 571) and which disappears already in later larval stages, is considered by EDGEWORTH to be the homologue of the connection in Anuran tadpoles formed by the commissura quadrato-cranialis anterior. The lateral connection ("palato-nasale Verbindung", STADTMÜLLER 1936, p. 568), which is known only in the adult *Ranodon sibiricus* (WIEDERSHEIM 1877, pl. 23, figs. 69—70), does not arise, as shown by EDGEWORTH (1925, p. 230) and STADTMÜLLER (1936, p. 571), until during the adult life after the disappearance of the medial larval connection. This lateral connection is highly suggestive of the connection found in advanced Anuran tadpoles between the processus quadrato-ethmoidalis palatoquadrati and the processus maxillaris posterior and which in them persists in the adults and forms the definitive connection between the palatoquadrate and the postero-ventral corner of the postnasal wall.

HIGGINS (1920, pp. 22—24, 62; pl. 4, figs. 23, 24) who first detected the larval medial connection between the palatoquadrate and the ethmoidal region of Urodeles in *Cryptobranchus* (*Menopoma*) *alleghaniensis*, is of opinion that this connection corresponds to the definitive (palatonasal) one in *Ranodon*. According to him there is thus only one connection between the palatoquadrate and the ethmoidal region in Urodeles, a connection which is most closely comparable to the definitive connection in *Anura*. PUSEY (1938, pp. 526—527), who has recently criticized EDGEWORTH'S opinion that the medial larval connection in Urodeles is the homologue of the connection by the commissura quadrato-cranialis anterior in Anuran tadpoles, seems also to doubt the existence of two different connections between the palatoquadrate and the ethmoidal region in Urodeles.

In agreement with EDGEWORTH, I am of opinion, however, that the two connections in Urodeles now under consideration are of different origin as are the corresponding ones in *Anura*. That this must be so is, it appears to me, evidenced by the circumstance that in *Ranodon* the medial larval connection disappears even before the stage at which the lateral definitive one begins to develop.

We shall now proceed to a closer examination of the two connections in Urodeles and to a comparison between them and the similarly situated ones in Anurans.

Both in Urodeles and Anurans two anterior processes, one antero-medial and one antero-lateral[1], may be distinguished in the palatoquadrate.

The antero-medial process in Urodeles arises already in very early embryonic stages and in these stages its longitudinal axis passes from behind and laterally in a direction forwards and medially. It fuses with the trabecula at the very base of the lamina orbitonasalis. On its lower side there arises a dermal bone, the dermopalatine (cf. WINTREBERT 1922, figs. 1, 4, 27—32, 53 and EDGEWORTH 1923, figs. 1—4, 8—10; 1925, pl. 14, fig. 58; pl. 15, figs. 60, 61). Up to these stages in its development the process agrees essentially with the similarly situated commissura quadrato-cranialis anterior (cf. p. 319 below) in Anuran tadpoles, and its embryonic development is thus a strong support for the opinion maintained by EDGEWORTH that it is a true homologue of the said process in Anurans.

In later embryonic stages, on the other hand, the antero-medial process in question undergoes somewhat different changes in Urodeles and Anurans. For a better understanding of these changes in Urodeles it is most appropriate first to turn to the Anurans.

The antero-medial process (the commissura quadrato-cranialis anterior) of the palatoquadrate in advanced Anuran tadpoles has an almost transverse position so that its anterior margin is situated immediately below the ventral margin of the lamina orbitonasalis. According to researches recently carried out by REINBACH (see p. 322 below) it fuses with the lamina orbitonasalis, but is not resorbed underneath this lamina, as has previously generally been assumed. Owing to this fusion of the process with the lamina orbitonasalis the palatoquadrate appears to be connected anteriorly only with the lateral end of the lamina orbitonasalis. The dermopalatine (*Dpl*, fig. 23 B), which is developed as a dermal bone on the lower side of the antero-medial process, persists also in adult Anurans.

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[1] The antero-lateral process is regarded by PUSEY (1938, pp. 526—531) as the true anterior end of the palatoquadrate. The antero-medial process is according to PUSEY the basal process of the palatoquadrate and has secondarily shifted forwards. EDGEWORTH maintains, on the other hand, that it is the antero-medial process that forms the true anterior end of the palatoquadrate, whereas the antero-lateral one in his opinion is a formation *sui generis* that "might have a new name" (EDGEWORTH 1925, p. 234). As will be demonstrated below (pp. 412, 521—522) the two processes here in question in Anurans and presumably also in Urodeles are both of them simply to be explained as derivates of the broad anterior end (the pars autopalatina) of the palatoquadrate of Rhipidistid Crossopterygians. The interpretation of the antero-medial process as a basal process advanced by PUSEY is untenable from all points of view (cf. p. 525 below).

In the majority of the Urodele larvae in which it has hitherto been described, viz. in *Ambystoma*, *Desmognathus*, *Spelerpes*, *Salamandrella* (*Hynobius*, cf. p. 399, foot-note 1) and *Ranodon* the antero-medial process is not developed "beyond the stage of a cellular strand" and disappears already during the embryonic development (EDGEWORTH 1925, pp. 227—233). In the larvae of certain other Urodeles (*Hynobius*, *Cryptobranchus alleghaniensis* and *Megalobatrachus japonicus*) the palatoquadrate becomes chondrified also in its antero-medial process which retains in them its connection with the ethmoidal region throughout the larger part of the larval period. The advanced larvae of these latter Urodeles exhibit an interesting condition, the palatoquadrate bar in them seemingly being connected anteriorly with the middle or even the lateral part of the lamina orbitonasalis (HIGGINS 1920, pl. 4, figs. 23, 24; EDGEWORTH 1923, figs. 1, 2, 4; AOYAMA 1930, figs. 5, 10, 11). This seems to indicate that the antero-medial process of the palatoquadrate here has a transverse position similar to that in advanced Anuran tadpoles and that as in these it becomes fused with the ventral margin of the lamina orbitonasalis. A further support for this is found in the position of the dermopalatine. According to AOYAMA (1930, p. 126) this bone is in advanced larvae of *Megalobatrachus* situated on the lower side of the so-called lamina orbitonasalis ("processus antorbitalis"). During the later part of the larval period the anterior part of the palatoquadrate bar in *Megalobatrachus* is completely resorbed and the palatoquadrate in *Megolobatrachus* does not, therefore, extend as far forwards as to the ethmoidal region. In connection with the reduction of the anterior part of the palatoquadrate bar the dermopalatine in *Megalobatrachus* is also completely reduced (AOYAMA 1930, pp. 174—175; cf. WINTREBERT 1922). This condition renders it very likely that in *Megalobatrachus* also the antero-medial process of the palatoquadrate disappears and that the postnasal wall in the adult *Megalobatrachus*, contrary to what is the case in Anurans, therefore, does not include any palatoquadrate component.

As already alluded to above, the dermopalatine is present in Urodeles in general during the larval period and then, as in *Megalobatrachus*, disappears completely towards the end of that period. It is still imperfectly known both as to shape and position. At least in certain forms it is situated on the lower side of the lamina orbitonasalis, as it is in *Megalobatrachus*. This is the case for instance in *Ambystoma* (Wintrebert 1922, figs. 27—30) where the antero-medial process does not develop beyond the procartilaginous stage, and in *Salamandra* (Wintrebert 1922, figs. 3—6, 53; Stadtmüller 1924, figs. 2, 5) in which no connection has so far been observed between the palatoquadrate and the ethmoidal region. As is well known, the dermopalatine is a dermal bone on the foremost part of the ventral side of the palatoquadrate. The fact that it is developed in larval stages of Urodeles in general thus seems to show that in younger larvae of Urodeles at least a mesenchymatic vestige of the antero-medial process of the palatoquadrate is present between the dermopalatine and the lower margin of the lamina orbitonasalis. Thus there is reason to assume that in Urodeles in general the palatoquadrate extends forwards to and is connected with the ethmoidal region during the earlier part of the larval period, but that its anterior part with the dermopalatine is then completely reduced during the later part of the larval period.

The antero-lateral process of the palatoquadrate in Urodeles which is hitherto known only in *Ranodon* does not arise until late during the embryonic development. It has been described by Edgeworth in a young individual in which it was found to form the foremost and some what laterally-curved end of the palatoquadrate bar. As in this individual it does not reach quite so far forwards as to the ethmoidal region, Edgeworth concludes that the process does not acquire its definitive connection with the ventro-lateral corner of the postnasal wall until in the adult (Edgeworth 1925, p. 230).

The antero-lateral process (the processus quadrato-ethmoidalis) of the palatoquadrate in *Anura* in several respects resembles the corresponding process in *Ranodon* described above. As that process, it does not arise until in very advanced larval stages. Quite as the said process in Urodeles it forms also the somewhat laterally-curved anterior end of the palatoquadrate bar, a condition well demonstrated in a figure given by Gaupp (1893, pl. 15, figs. 25, 26; cf. Pusey 1938, pl. 41, fig. 19) of a transforming larva of *Rana*. Later on it fuses with the ventro-lateral corner of the postnasal wall, forming the definitive connection between the palatoquadrate and the ethmoidal region in the same way as in *Ranodon*.

Since it is thus clear that they agree with one another not only in position, but also in embryonic development, we are fully justified in concluding that the antero-lateral process in *Ranodon* and the antero-lateral process in Anurans are strictly homologous formations.

To summarize the above discussion, the palatoquadrate in Urodeles may have two different connections with the ethmoidal region, a medial larval one and a lateral definitive one, in all probability corresponding exactly to the connections in Anurans formed by the commissura quadratocranialis anterior and the processus quadrato-ethmoidalis respectively. As we have also seen, the palatoquadrate in Urodeles is normally much reduced anteriorly. In view of the presence of the dermopalatine in larval stages, it is likely that the palatoquadrate, represented anteriorly by mesenchyma or procartilage, extended as far forwards as to underneath the lamina orbitonasalis, whereas in later larval stages it is reduced anteriorly together with the dermopalatine and in adults, *Ranodon* excepted, it ends behind the ethmoidal region (cf. p. 412 below).

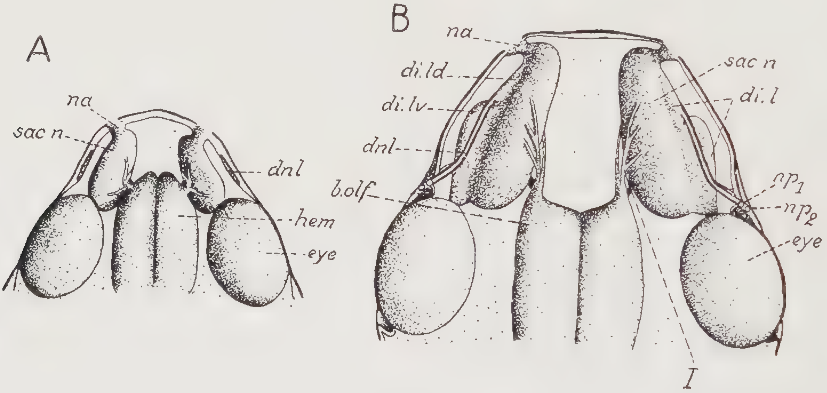

Fig. 19. *Triturus (Triton) alpestris.* Diagram of the forebrain, nasal sacs and eyes in dorsal view. *A*, larva 23 mm, *B*, larva, 38 mm, at the end of the metamorphosis. From Schuch (1934, figs. 39 a and 1).

b. olf, bulbus olfactorius; *di. l*, lateral diverticle of nasal sac; *di. ld*, *di. lv*, dorsal (anterior) and ventral (posterior) divisions respectively of lateral diverticle; *dnl*, ductus nasolacrimalis; *hem*, hemisphere of forebrain; *na*, anterior external nostril; np_1, np_2, posterior openings of nasolachrymal duct (posterior external nostrils); *sac n*, nasal sac; *I*, n. olfactorius.

The intermaxillary gland (*gl. imx*, fig. 18) in Urodeles (Wiedersheim 1876; Seifert 1932; Francis 1934; Fahrenholz 1937; cf. pp. 400—401) is generally strongly developed and occupies the cavum internasale and cavum prenasale where it extends upwards as far as to underneath the skin of the dorsal side of the head. It discharges by one or several openings into a small median depression on the roof of the mouth immediately beneath the gland.

The nasal sac of the Urodeles is most completely known in *Triturus* (*Triton*; Seydel 1895; Matthes 1927, 1934; Schuch 1934; Schultze 1937; see also Watanabe 1934, 1934 a, 1935, 1935 a; Fukuchi and Sisido 1936, and Kudo 1927). In this form it seems in the main to agree with the nasal sac in *Salamandra* (Matthes 1934, p. 894) and is as follows (*sac n*, fig. 19; cf. fig. 18). It consists of a main medial part enclosing the main cavity and a lateral narrower part, the lateral diverticle (*di. l*). The main part, which is considerably larger than the lateral diverticle, is provided with two openings connected by short tubes with the anterior external nostril (*na*) and the internal nostril or choana respectively. The lateral diverticle is composed of two divisions, one dorsal and one ventral. The dorsal division (*di. ld*) forms the anterior part of the lateral diverticle and has therefore usually been considered an anterior part of that diverticle (e. g. MATTHES 1934, pp. 893—894). However, it is fairly clear that it lies dorsally to the anterior parts of the crista rostro-caudalis and the plica rostro-caudalis (*ri. w. al*). It extends from a point immediately behind the origin of the anterior nasal tube backwards approximately to the anterior end of the ventral division of the diverticle. Its posterior end is not directly continuous with the anterior end of the ventral division, but is situated dorsally to that division and separated from it by the crista rostro-caudalis and the plica rostro-caudalis (*ri. w. al*). The dorsal division is continued backwards by the posterior nasal tube or nasolachrymal duct (*dnl*) which goes backwards dorsally to the ventral division of the diverticle, but is separated from this by the lateral wall of the nasal cavity (cf. MATTHES 1934, fig. 684). The ventral division (*di. lv*, fig. 19 B; cf. fig. 18 A, B, *Jo*) of the diverticle is low and lies in the lateral recess of the nasal cavity. It consists of sensory epithelium and forms the so-called Jacobson organ. Anteriorly it protrudes as a shallow bulge ending blindly. Posteriorly it passes over into the mucous membrane of the palate and there forms a distinct fold, the plica palatina ("laterale Gaumenfalte"; cf. e. g. SEIFERT 1932, fig. 5; BARGE 1937, fig. 27), postero-laterally to the choana. This fold is supported by Seydel's palatal process and parts of the vomer and maxillary (pars palatina, Mx_3, fig. 16 B, C). It forms the ventral boundary of a groove opening medially, the sulcus maxillo-palatinus ("Seitliche Gaumenrinne"), which constitutes the posterior prolongation of the lumen, the sinus lateralis nasi (*sin. l*, fig. 18 C; "seitliche Nasenrinne"), of the ventral division of the lateral diverticle of the nasal sac. The so-called Jacobson organ is thus by means of this groove in communication posteriorly with the mouth cavity.

The forebrain and the olfactory nerve in Urodeles have been treated in several forms (*Salamandra*, KUHLENBECK 1921, pl. 21, fig. 1; FRANCIS 1934; *Triturus*, BURCKHARDT 1891; G. M. SMITH 1927, pl. 8, fig. 30; BENEDETTI 1928, figs. A—E; pl. 1; *Desmognathus*, FISH 1895; *Ambystoma*, BINDEWALD 1914; HERRICK 1910, 1938, 1938 a, 1938 b, 1939; *Megalobatrachus*, KUDO 1927; IKEDA 1931; *Hynobius*, SUMI 1926; *Necturus*, KINGSBURY 1895; *Proteus*, BENEDETTI 1933). The hemisphere (*hem*, figs. 19, 21)

is oblong and separated from its antimere by a narrow median slit. The bulbus olfactorius (*b. olf*) lies close to the antero-ventro-lateral part of the hemisphere of its side and is continuous with it without any distinct line of demarcation. The tractus olfactorius is situated in the lateral wall of the hemisphere and extends backwards as far as to the habenular region (BENEDETTI 1928, p. 53). The olfactory nerve (*I*) is comparatively short and in adults it passes out from the ventral part of the apical end of the bulbus olfactorius. In the larvae, on the other hand, where the forebrain extends forwards between the nasal sacs, it leaves the bulbus olfactorius towards the lateral side.

The nerves of the snout in Urodeles have been described by several writers (PLESSEN and RABINOVICZ 1891; H. H. WILDER 1892; HERRICK 1894; BOWERS 1900; COGHILL 1902, 1906; KINGSLEY 1902; DODDS 1906; NORRIS 1908, 1913; G. M. SMITH 1927; GÖPPERT 1928, 1929; BENEDETTI 1933; FRANCIS 1934). The description below is based mainly on the detailed account of them in *Salamandra* as given by FRANCIS.

The r. ophthalmicus superficialis V is weakly developed in *Salamandra* where it does not extend forwards as far as to the snout (GÖPPERT 1928, fig. 2; 1929, fig. 6; FRANCIS 1934, p. 139). In the larval *Salamandra* it is joined by a strong r. ophthalmicus lateralis (PLESSEN and RABINOVICZ 1891, pls. 1, 2, r. frontalis; GÖPPERT 1928, fig. 1; 1929, figs. 2, 3) which is traceable as far forwards as almost opposite the external nostril. In *Siren*, where it is better known than in *Salamandra*, the r. ophthalmicus lateralis passes laterally to the profundus branches that have their passage dorsally to the nasal capsule (NORRIS 1913, figs. 4—6; cf. NORRIS 1908, pl. 5, figs. 2, 3).

The n. profundus (*n. pr*, figs. 20, 21) is very strongly developed. It gives off two dorsal branches[1] in the orbit fairly far behind the snout. The anterior dorsal branch (*n. prd*), which bifurcates almost immediately, is "distributed to the skin covering the fronto-ethmoidal region, and thus would appear to be the equivalent of the *RR. frontales et palpebrales superiores anteriores* (GAUPP) of the Frog" (FRANCIS 1934, p. 140). In Amphiuma (NORRIS 1908, pl. 5, figs. 2, 3) twigs of this nerve pass both medially to and together with the r. ophthalmicus lateralis, and in *Siren* (NORRIS 1913, figs. 5—6, *op*) such twigs are found medially to the r. ophthalmicus lateralis.

After giving off the two dorsal branches just referred to and after arriving about midway in the orbit, the n. profundus in *Salamandra* as well as in other Urodeles (NORRIS 1913, p. 279) breaks up into three terminal branches, a medial (*n. 5a. M*), a lateral (*n. 5a. L*), and a ventral one (*n. 5a. V*, figs. 20, 21). The course of these three branches in *Salamandra* is described by FRANCIS (1934, pp. 141—142) as follows. "The mesial terminal branch (*n. 5a. M.*) passes through the Foramen orbitonasale mediale in the antorbital cartilage slightly dorsal to the origin of the M. obliquus superior. On entering the nasal capsule the nerve turns mesially and then anteriorly, passing over the nasal sac dorsal to the olfactory nerve. At a point a little posterior to the level of the external nares it breaks up into several fine terminal twigs which penetrate formina in the premaxilla and the nasal bone, and supply the skin of the snout".

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[1] These two branches probably belong to the r. frontalis (portio ophthalmici profundi), whereas the other parts of the nerve constitute the r. ophthalmicus profundus (r. nasalis).

"Just before this branch enters the For. orbito-nasale mediale, while it is still within the orbit, it gives a small lateral branch which fuses with a twig from the lateral terminal branch and then enters the nasal capsule separately from the main nerve. It passes dorsal to the nasal sac, and turns first mesially, then sharply laterally, and finally perforates the nasal capsule laterally to supply the skin near the ductus nasolacrimalis".

"The lateral terminal branch (*n. 5a. L.*) gives off one or two small twigs within the orbit which turn sharply lateralwards, and supply the skin over the upper jaw near the anterior angle of the orbit. The main nerve then itself turns lateralwards, penetrates the For. orbito-nasale laterale, and enters the postero-lateral corner of the nasal capsule. It crosses the corner of the capsule obliquely, more or less lateral to the olfactory epithelium, and passes through the fenestra infraconchalis and then through foramina in the maxilla to supply the skin of the face laterally of the nasal capsule".

"The ventral terminal branch (*n. 5a. V.*) enters the nasal capsule by the For. orbito-nasale mediale directly between the origins of the superior and inferior oblique muscles, a little ventral to the mesial terminal branch, and close to the floor of the capsule. After passing through the foramen the nerve remains entirely ventral to the olfactory epithelium and, turning slightly mesially anastomoses with the R. palatinus VII just mesial to the internal narial opening. In sections ganglionic cells are discernible at the point where these two nerves join, and even in dissections a swelling suggestive of a ganglion is noticeable. The nerves resulting from this fusion are of course mixed, and contain both trigeminus and facialis fibres, so that is is not possible to determine the precise distribution of each component by dissection. In general they spread over the roof of the mouth under the nasal organs".

As is obvious from the statements above, the n. profundus in Urodeles has a wider area of distribution in the snout than the corresponding

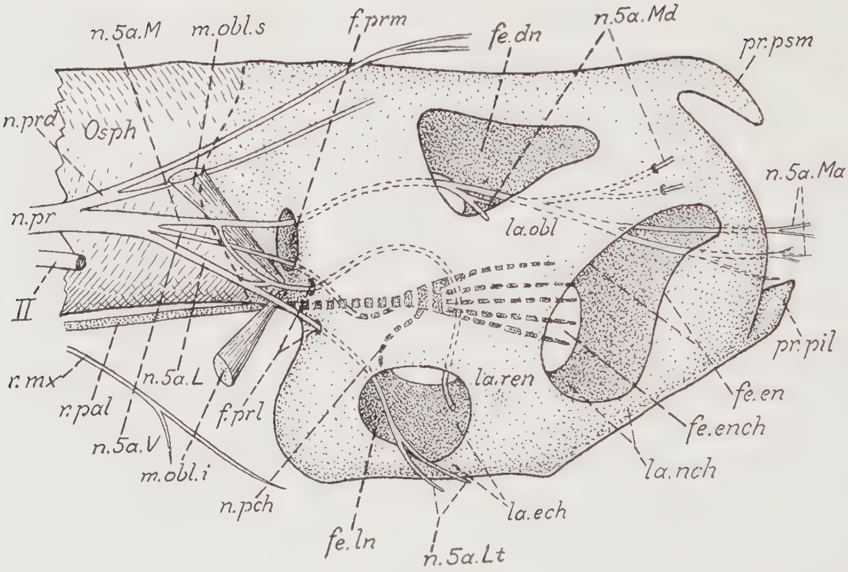

Fig. 20. Adult *Salamandra salamandra (maculosa)*. Diagram of the oblique eye muscles and the cranial nerves of the snout, showing their relation to the endocranium. Lateral view. Compilation after the descriptions and figures given by Francis (1934).

Osph, orbitosphenoid; *fe. dn,* fenestra dorsalis nasi; *fe. en,* fenestra endonarina communis; *f. ench,* fenestra endochoanalis; *fe. ln,* fenestra lateralis nasi (fenestra infraconchalis); *f. prl, f. prm,* lateral and medial profundus foramen; *la. ech,* lamina ectochoanalis; *la. nch,* lamina nariochoanalis; *la. obl,* lamina obliqua; *la. ren,* lamina retronarina; *m. obl. i, m. obl. s,* m. obliquus inferior and m. obliquus superior; *n. pch,* postchoanal nerve; *n. pr,* n. profundus; *n. prd,* dorsal branch of n. profundus; *n. 5a. L,* lateral terminal branch of n. profundus; *n. 5a. Lt,* terminal twig of lateral terminal profundus branch; *n. 5a. M,* medial terminal branch of n. profundus; *n. 5a. Ma, n. 5a. Md,* anterior and dorsal twigs of medial terminal profundus branch; *n. 5a. V,* ventral terminal branch of n. profundus; *pr. pil,* processus prenasalis inferior lateralis; *pr. psm,* processus prenasalis superior medius; *r. mx,* r. maxillaris V; *r. pal,* r. palatinus VII; *II,* n. opticus.

nerve in Elasmobranchs, Brachiopterygians (*Polypterus*), Actinopterygians, Dipnoans, and Anurans. Contrary to what is the case in the said groups it also innervates most of the lateral parts of the snout.

The r. maxillaris V (*r. mx,* fig. 20) is a weak nerve in both *Salamandra* (Francis 1934, p. 143; Göppert 1928, fig. 2; 1929, figs. 6, 7) and other Urodeles (*Ambystoma tigrinum,* Coghill 1902, pp. 224, 258—262; *Plethodon,* Dodds 1906, fig. 2; *Spelerpes,* Bowers 1900, p. 184; *Amphiuma,* Norris 1908, p. 538) and ends about at the antero-ventro-lateral corner of the orbit. It thus extends only slightly forwards into the snout, which is mainly or almost entirely innervated by the n. profundus instead of by the r. maxillaris V. The strong nerve-branch in *Ambystoma punctatum* described by Herrick (1894, p. 201, pls. 19, 20) as the r. maxillaris seems mainly to be the r. buccalis lateralis, whereas the r. maxillaris of Benedetti's description (1933, p. 57; pl. 13, figs.

64, 65, *ra. V. mx*) of *Proteus* is probably a branch of the n. profundus.

The weak development and slight forward extent of the r. maxillaris V are features particularly characteristic of the Urodeles, which in this respect, as well as in the strong development of the n. profundus, differ considerably from Elasmobranchs, Brachiopterygians (*Polypterus*), Actinopterygians, Dipnoans and Anurans.

As the r. ophthalmicus lateralis, the r. buccalis lateralis is in *Salamandra* present only in the larvae. Judging from the figures given by Plessen and Rabinovicz (1891, pls. 1, 2, r. maxillaris superior; cf. also Göppert 1929, figs. 2, 3, N. maxillaris) it passes in the larval *Salamandra* laterally to the nasal sac. In *Siren* where it persists also in the adults and where it has been described in detail by Norris (1913, p. 294) it breaks up into three branches, all supplying organs of the infraorbital sensory line situated in the snout. One of these branches, "the buccalis proper", (*buc. 1*, Norris 1913, figs. 4—6; pl. 1) runs forwards in the upper lip, innervating the sensory line organs as far forwards as to opposite the external nostril. The infraorbital sensory organs of the foremost part of the snout are innervated by the second branch (*buc. 2*, Norris 1913, p. 293). This branch leaves the truncus infraorbitalis far back in the orbit, more precisely underneath the posterior part of the eye bulb. In order to reach its sensory organs it traverses the nasal cavity medially to the choana and ventro-medially to the nasal sac. In *Amphiuma* (Norris 1908, p. 536; pl. 4; pl. 5, figs. 2, 3) the foremost sensory canal organs of the snout are innervated by a buccalis branch, which contrary to what is the case in *Siren*, seems to pass laterally to the choana. Finally, the third buccalis branch in *Siren* (*buc. 3*, Norris 1913, p. 294, figs. 5, 6; pl. 1) goes forwards laterally to the lower margin of the postnasal wall thence curving upwards to find its ultimate ending immediately above the external nostril. It is said to innervate sensory canal organs ("neuromasts") "of the infraorbital series which extend from the ventral border of the eye anteriorly just over the nostril". As is thus obvious there is in *Siren* between the ventral border of the eye and the external nostril a special line of sensory organs forming an obliquely antero-dorso-medial branch of the infraorbital line proper.

The r. palatinus VII (*r. pal*, figs. 20, 21) in *Salamandra* gives off a fine lateral branch in the orbit. The further course of the nerve in *Salamandra* is described by Francis (1934, p. 145) as follows. "The main palatine nerve continues along the dorsal side of the pre-vomer, passing between it and the 'Planum internasale', and enters the nasal capsule through the fenestra basalis. Here it is immediately joined by the ventral terminal branch of the ophthalmicus profundus V at the mesial border of the internal narial opening. At the junction of these two nerves a fairly conspicuous ganglion occurs. A number of fine twigs are given off by the combined nerve, most of which pass anteriorly mesial to the internal narial opening, and spread over the roof of the mouth ventral to the olfactory epithelium, and ventral to the branches of the olfactory nerve. One branch, however, is given off laterally and passes round the posterior border of the internal nares where it is joined by the lateral palatine nerve — when such is present — to form the *post choanal nerve*" (*n. pch*, figs. 20, 21 in the present work).

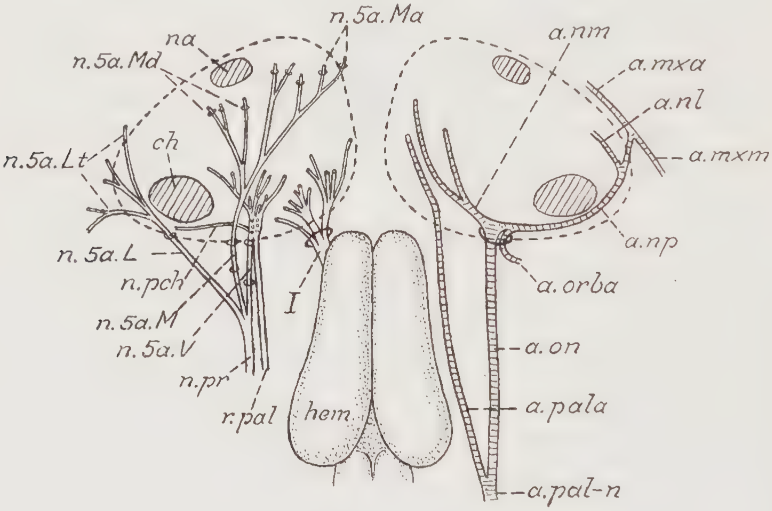

Fig 21. *Salamandra salamandra* (*maculosa*). Diagram of the forebrain, nerves and arteries of the snout. Dorsal view. Compilation after the descriptions and figures given by Francis (1934).

a. mxa, a. mxm, anterior and medial maxillary artery; *a. nl, a. nm, a. np,* lateral, medial, and posterior nasal artery; *a. on,* orbitonasal artery; *a. orba,* anterior orbital artery; *a. pala,* anterior palatine artery; *a. pal-n,* palatonasal artery; *ch,* choana; *hem,* hemisphere of forebrain; *na,* anterior external nostril; *n. pch,* postchoanal nerve; *n. pr,* n. profundus; *n. 5a. L,* lateral terminal branch of n. profundus; *n. 5a. Lt,* terminal twigs of lateral terminal profundus branch; *n. 5a. M,* medial terminal branch of n. profundus; *n. 5a. Ma, n. 5a. Md,* anterior and dorsal twigs of medial terminal profundus branch; *n. 5a. V,* ventral terminal branch of n. profundus; *r. pal,* r. palatinus VII; *I,* n. olfactorius.

As may be gathered from the brief account just given of the nerve supplies of the snout, the Urodeles differ clearly from the Elasmobranchs, Brachiopterygians (*Polypterus*), Actinopterygians, Dipnoans, and Anurans as regards the development and distribution of the n. profundus and the r. maxillaris V. The n. profundus is a large nerve in Urodeles. It supplies the snout not only anteriorly and dorsally, but also, in the main, laterally. The r. maxillaris V is thus in Urodeles almost entirely substituted in the snout by the n. profundus. The r. maxillaris V in Urodeles is, therefore, not only more weakly developed than the corresponding nerve in Elasmobranchs, Brachiopterygians, Actinopterygians, Dipnoans, and Anurans, but has also a much shorter forward extent than that nerve, finding its ultimate termination in the very hindmost part of the snout close in front of the orbit.

Correlative with its particular innervation, the snout in Urodeles is devoid of large vessels along its ventro-lateral margin. More precisely there are no vessels comparable to a maxillary artery and a maxillary vein. The main vessels of the snout in Urodeles all enter and leave the ethmoidal region medially to the lateral border and the postero-latero-ventral corner of the postnasal wall.

The exact course and topographical relations of the vessels of the snout in *Salamandra* and other Urodeles (Bethge 1898; Osawa 1902; Seelye 1906) are still imperfectly known. From the description of *Salamandra* given by Francis (1934) it is obvious, however, that the blood is carried to the snout mainly through one artery, the a. orbitonasalis (*a. on*, fig. 21), which "passes obliquely in an antero-dorsal direction across the surface of the orbitosphenoid to the dorsal side of the inner anterior angle of the orbit" (Francis 1934, p. 203). This artery, which is the terminal branch of the palatonasal artery (*a. pal-n*, fig. 21)[1], passes, as pointed out by Francis, ventrally to the eye muscles and must therefore not be confused with the a. orbitonasalis of the frog which has its passage dorsally to the said muscles. The artery in question enters the nasal capsule by a foramen in the postnasal wall. Francis does not state anything more definite regarding the position of this foramen in *Salamandra*, but Chung (1931, p. 379) says that in the Japanese Urodele forms studied by him the lateral profundus foramen (the "foramen orbitonasale laterale") is traversed by large vessels and that this applies also to *Salamandra*. According to the statement by Francis quoted above it is probable, however, that in *Salamandra* it reaches the nasal cavity through the medial profundus foramen and not through the lateral one. It may possibly be the v. nasalis (see below) that leaves the ethmoidal region through one of the lateral profundus foramina (cf. FRANCIS 1934, pl. 13, fig. 58). Within the nasal capsule the a. orbitonasalis bifurcates into a medial nasal artery (*a. nm*, fig. 21) and a posterior nasal artery (*a. np*). The latter artery breaks up into four branches, three of which, viz. the lateral nasal (*a. nl*), the medial maxillary (*a. mxm*), and the anterior maxillary (*a. mxa*) arteries, go to the lateral parts of the nasal cavity and to the upper lip. The foremost part of the palate is supplied with blood through a special branch of the palatonasal artery, the anterior palatine artery (*a. pala*, fig. 21).

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[1] Francis (1934, p. 201; pl. 13, fig. 58; pl. 14, fig. 61) says that the a. ophthalmica superior anterior "fuses with a branch of the palatonasal artery and enters the nasal capsule", but whether this fusion takes place with the orbitonasal artery is not stated. It is likely, however, that this is so. The part of the orbitonasal artery in *Salamandra* entering the nasal cavity is presumably, therefore, formed by a fusion of the a. ophthalmica superior anterior with a branch of the a. palatonasalis.

The blood of the snout in *Salamandra* is received by the following veins: a v. frontalis passing dorsally to the nasal capsule, a v. nasalis coming from the interior of the nasal capsule, a v. maxillopalatina originating in the upper lip, and a v. palatina taking its origin from the anterior part of the palate. The v. cerebralis anterior is absent in adult Urodeles (v. GELDEREN 1924, pp. 567—572).

The particular development of the nerves and vessels of the snout in Urodeles might be suspected to have arisen in consequence of the reduction of the anterior parts of the palatoquadrate (cf. pp. 295—300) but that this cannot be so is shown, as we shall find, by the conditions in the *Porolepiformes* among the Crossopterygians (cf. pp. 412—413).

F. Anura, with special reference to Rana.

The account of the structure of the snout in Anurans refers above all to the conditions in *Rana*, particularly the two European species *R. fusca* (*temporaria*) and *R. esculenta*.

The main sources for our knowledge of the skeleton and general anatomy of the snout in *Rana* are papers and works by DUGÈS (1835), W. K. PARKER (1871, 1876, 1881), HOFFMANN (1873—1878), BORN (1876), PARKER and BETTANY (1877), GAUPP (1893, 1905), SEYDEL (1895), ECKER-WIEDERSHEIM-GAUPP (1896, 1899, 1904), MCCOTTER (1917), BHATIA and PRASHAD (1918), PROCTER (1919), C. A. DU TOIT (1933), RAMASWAMI (1935), STADTMÜLLER (1936), DE BEER (1937) and others. Embryological studies of the skeleton have been carried out inter alia by GAUPP (1893, 1905), SPEMANN (1898), PEETERS (1910), and PUSEY (1938), and of the olfactory organ by HINSBERG (1901).

The following description of the skeleton of the snout in *Rana* is based mainly on the works by GAUPP and ECKER-WIEDERSHEIM-GAUPP supplemented to some extent by observations undertaken on an alizarine preparation of *R. esculenta* made by the present writer.

The ethmoidal region consists mainly of cartilage. Its postero-median part, however, is occupied by the foremost portion of the unpaired sphenethmoid bone (*Set*, figs. 23, 24) whose larger posterior portion lies in the adjacent anterior parts of the orbitotemporal region.

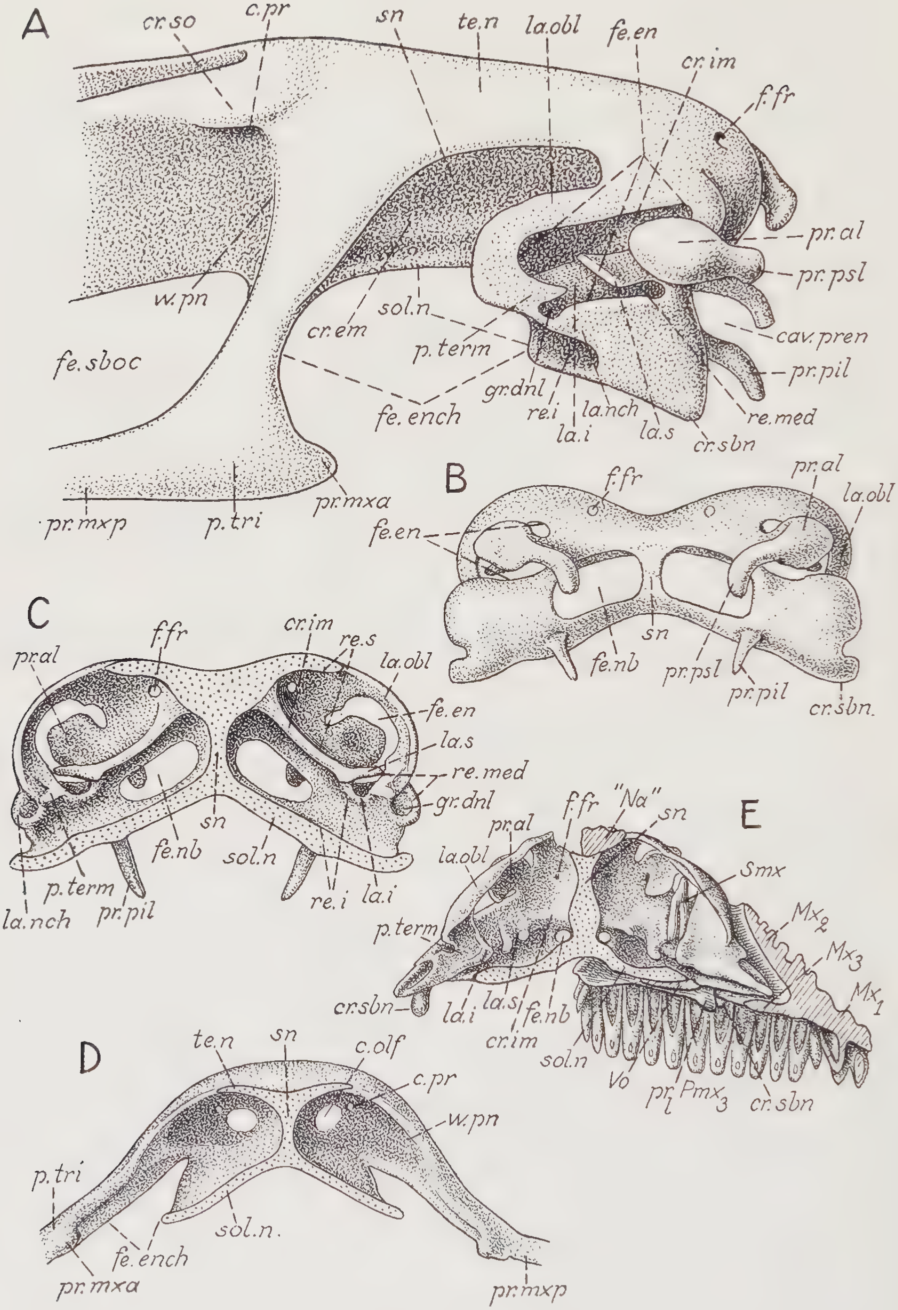
The internasal wall is a narrow septum nasi (*sn*, figs. 22, 25, 27) separating the large nasal cavities. Posteriorly the septum nasi is continued by a thin septum (*s. olf*, figs. 23 A, 24 A) between the canales olfactorii. This latter septum extends backwards to the transition between the ethmoidal and orbitotemporal regions. The cranial cavity thus does not stretch forwards into the ethmoidal region and consequently has no ethmoidal part.

Underneath the internasal wall and nasal capsules there is a median unpaired depressed space, the cavum subnasale (*cav. sbn*, fig. 23 B; cf. fig. 72 C), which houses a posterior portion of the intermaxillary gland. This space is bounded dorsally and dorso-laterally by the internasal wall and the solum nasi respectively (cf. figs. 22 B—D, 27 A) and ventrally by the mucous membrane of the mouth cavity, whereas anteriorly it is continuous with the cavum prenasale. It is considerably broader than the internasal wall and highest in its anterior median part, thence decreasing in height both laterally and posteriorly.

The divisio prenasalis communis has a somewhat larger rostro-caudal extent than in *Salamandra*. Its skeleton is very imperfect, being represented only by the prenasal walls of both sides and three paired processes. The processes form a support for the "premaxillary" (cf. pp. 497—498). Two of them, the processus prenasalis inferior lateralis (*pr. pil*, figs. 22 A—C, 23 B, 25 A, 31; cf. figs. 67 C, 72 C) and the processus prenasalis superior lateralis (*pr. psl*), are slender bars of cartilage, curved somewhat ventrally anteriorly, which protrude from the antero-medial part of the solum nasi and the dorso-lateral part of the prenasal wall respectively. The third of the processes in question, the crista subnasalis (*cr. sbn*, fig. 22 A, B, E), is made up of the ventro-lateral corner of the prenasal wall and projects in a ventral and slightly anterior direction. The three processes traverse an unpaired median and fairly large space, the cavum prenasale (*cav. pren*, figs. 22 A, 23 B; cf. fig. 72 C), which is situated in the divisio prenasalis communis. This space houses the main anterior part of the intermaxillary gland. It has imperfect dorsal, anterior, lateral, and ventral boundaries formed by the "premaxillaries". Posteriorly it is bounded by the septum nasi and the prenasal walls, but below these it is there in open communication with the cavum subnasale.

We shall now proceed to the description of the nasal cavity, beginning with its anterior and most complicated half.

The walls of the anterior half of each nasal cavity are pierced not only by the anterior parts of the fenestra endochoanalis and fenestra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fe.ench
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fe.sboc
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cr.sbn
D
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c.olf
c.pr
w.pn
p.tri
sol.n.
fe.ench
pr.mxa
pr.mxp

Fig. 22. *A—D*, *Rana fusca*. *A*, anterior part of the endocranium of young animal in lateral view. About $^{27}/_{1}$. From Ecker-Wiedersheim-Gaupp (1904, fig. 146). *B*, and *C*, anterior half of the ethmoidal region of larva towards the end of the metamorphosis, in anterior and posterior views. About $^{33}/_{1}$. From Gaupp (1893, pl. 15, figs. 31 and 32),

nasolateralis (see pp. 313—314), but also by three other openings, a small foramen frontale and two fairly large fenestrae, the fenestra nasobasalis and the fenestra endonarina communis.

The foramen frontale (*f. fr*, figs. 22 A—C, 29, 30) is situated in the foremost medial part of the tectum nasi near the transition between the tectum nasi and the prenasal wall. It is traversed by the r. externus narium of the n. profundus which emerges from the nasal cavity.

The fenestra nasobasalis (*fe. nb*, fig. 22 B, C) perforates the ventromedial part of the prenasal wall and connects the recessus inferior of the nasal cavity with the cavum prenasale. It gives passage to the r. medialis narium of the n. profundus and to certain tubes of the intermaxillary gland which extend backwards into the nasal cavity.

The fenestra endonarina communis (*fe. en*, fig. 22 A—C) lies in the lateral wall of the nasal cavity and extends as far forwards as to the prenasal wall which forms its anterior boundary. Anteriorly it is subdivided into a dorsal and a ventral part by the processus alaris (*pr. al*; cartilago alaris, Gaupp), a process directed posteriorly which issues from the anterior margin of the fenestra. This process which anteriorly passes over into the processus prenasalis superior lateralis constitutes a part of the lateral nasal wall. Antero-dorsally the fenestra in question is bounded by the lateral border of the tectum nasi and postero-dorsally and posteriorly by a curved bar of cartilage, the lamina obliqua (*la. obl*, figs. 22 A—C, 25 A, 30; cartilago obliqua, Gaupp), which is connected antero-dorsally with the tectum nasi and which like the processus alaris forms part of the lateral nasal wall. At its postero-ventral corner the fenestra has no definite boundary. It is continued there by a short groove (*gr. dnl*, fig. 22 A, C) running posteriorly in which the nasolachrymal duct leaves the nasal cavity. This groove is developed dorsally to the postero-lateral parts of the lamina inferior (see p. 312)

slightly altered. *D*, posterior half of the ethmoidal region of young animal in anterior view. Less than $^{20}/_{1}$. From Ecker-Wiedersheim-Gaupp (1896, fig. 22). *E*, *Calyptocephalus gayi*. Anterior half of the ethmoidal region with the dermal bones of right side. Metamorphosed animal. Posterior view. About $^{4}/_{1}$. From Reinbach (1939, fig. 9).

Mx_1, Mx_2, Mx_3, pars dentalis, pars facialis, and pars palatina of maxillary; "*Na*", "nasal"; *Smx*, septomaxillary; *Vo*, vomer; *cav. pren*, cavum prenasale; *c. olf*, canalis olfactorius; *c. pr*, profundus canal; *cr. em*, crest on dorsal face of solum nasi supporting the eminentia olfactoria; *cr. im*, crista intermedia; *cr. sbn*, crista subnasalis; *cr. so*, crista supraorbitalis; *fe. en*, fenestra endonarina communis; *fe. ench*, fenestra endochoanalis; *fe. nb*, fenestra nasobasalis; *fe. sboc*, fenestra subocularis; *f. fr*, foramen frontale; *gr. dnl*, groove for nasolachrymal duct; *la. i*, lamina inferior; *la. nch*, lamina nariochoanalis; *la. obl*, lamina obliqua; *la. s*, lamina superior; *pr. al*, processus alaris; pr_l Pmx_3, lateral process of pars palatina of "premaxillary"; *pr. mxa*, *pr. mxp*, processus maxillaris anterior and posterior; *pr pil*, processus prenasalis inferior lateralis; *pr. psl*, processus prenasalis superior lateralis; *p. term*, pars terminalis; *p. tri*, pars triangularis of postnasal wall; *re. i*, *re. med*, *re. s*, recessus inferior, medius, and superior of cavity of nasal capsule; *sn*, septum nasi; *sol. n*, solum nasi; *te. n*, tectum nasi; *w. pn*, postnasal wall.

and laterally to a mass of cartilage, the pars terminalis (*p. term*, fig. 22 A, C; cf. figs. 22 E, 67 C; planum terminale, GAUPP), that connects the ventral end of the lamina obliqua with the lamina inferior. The pars terminalis lies within the nasal cavity (see fig. 22 C) and thus does not belong to the actual lateral wall of the nasal cavity. As will be shown below (p. 514) it is presumably in part a new formation arisen in the Anurans, a formation which accordingly is devoid of a homologue in the piscine ancestors of the *Anura*. Finally the ventral boundary of the fenestra endonarina is formed by the antero-ventral part of the lateral nasal wall. This part of the lateral nasal wall separates the fenestra endonarina communis from the fenestra endochoanalis and thus represents the lamina nariochoanalis (*la.nch*, fig. 22 A, C).

On the medial part of the posterior face of the prenasal wall in the foremost part of the nasal cavity and thus above the fenestra nasobasalis, there is a marked crest. This crest, the crista intermedia (*cr.im*, fig. 22 A, C; cf. figs. 22 E, 70 C, 71 C), which is continuous dorsomedially with the septum nasi, runs laterally and somewhat downwards and posteriorly and is thus somewhat obliquely orientated. Its upper side faces dorso-laterally. The crest bifurcates ventro-laterally into two laminae, an upper and almost horizontal one, the lamina superior (*la.s*, figs. 22 A, C, 27 A, 29; cf. figs. 22 E, 67 C, 70 C, 71 C, 72 C), and a lower one, the lamina inferior (*la.i*, fig. 22 A, C, 27 A; cf. figs. 22 E, 67 C, 70 C, 71 C, 72 C), which is a straight prolongation of the crest itself. Whereas the crista intermedia has but a slight rostro-caudal extent, both the lamina superior and the lamina inferior extend considerably further backwards into the nasal cavity (cf. ECKER-WIEDERSHEIM-GAUPP 1904, figs. 139—141). The lamina superior is a plate of cartilage which ends free anteriorly, laterally, and posteriorly, with free antero-lateral, postero-lateral, and postero-medial margins. The two latter margins meet at a fairly pointed corner, situated at about the middle of the posterior part of the anterior half of the nasal cavity. The lamina inferior is anteriorly continuous with the prenasal wall, whereas posteromedially it has a free margin antero-medially passing over into the posterior margin of the crista intermedia. Laterally it is fused with the internal (medial) side of the lamina nariochoanalis somewhat below the dorsal border of that lamina (the ventral border of the fenestra endonarina communis). There is, therefore, immediately laterally to it a raised margin formed by the lamina nariochoanalis. It is the hinder part of this raised margin of the lamina nariochoanalis that constitutes the lateral boundary of the groove for the nasolachrymal duct (*gr.dnl*).

The anterior and lateral parts of the anterior half of the nasal cavity are subdivided by the crista intermedia, lamina superior, and lamina inferior and by a dermal bone, the septomaxillary (see pp. 317—319), into three divisions, the recessus superior, the recessus medius, and the recessus inferior.

The recessus superior (*re. s*, figs. 22 C, 29, 69; cf. figs. 71 C, 72 C; cavum superior GAUPP) lies dorsally to the crista intermedia, and dorsally also to the lamina superior and the septomaxillary. It is bounded dorsally, medially, and anteriorly by the tectum nasi, septum nasi, and prenasal wall, respectively. Laterally it opens outwards through the fenestra endonarina communis.

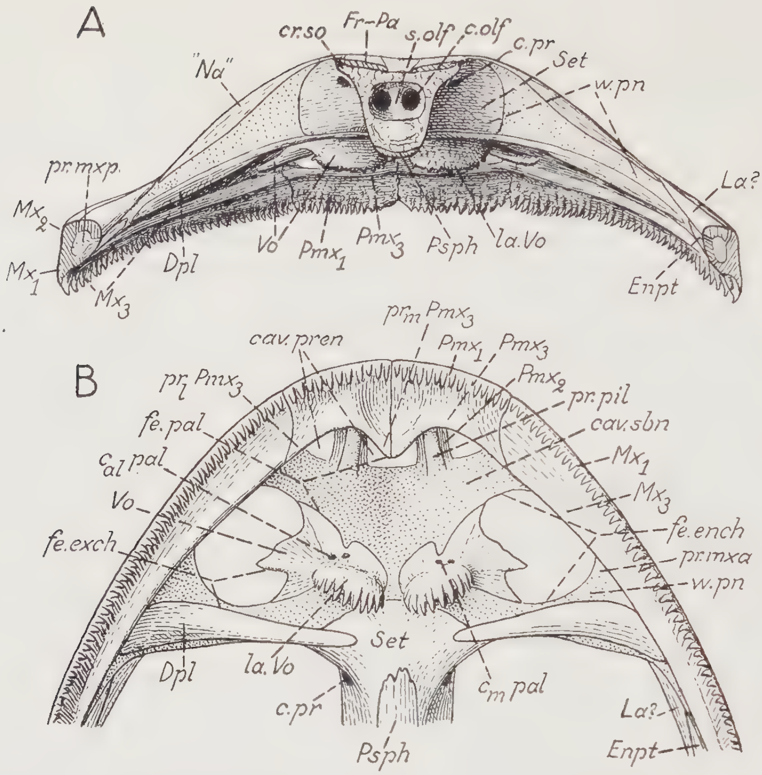
The recessus medius (*re. med*, figs. 22 A, C, 69; cf. figs. 71 C, 72 C; cavum medium, GAUPP) is situated between the lateral parts of the recessus superior and inferior and extends forwards to the prenasal wall. Its dorsal boundary is formed by the lamina superior and the septomaxillary and its ventro-medial boundary by the lamina inferior. Laterally it is bounded by the raised margin of the lamina nariochoanalis. The groove for the nasolachrymal duct (*gr. dnl*) leads backwards from the postero-lateral corner of the recess.

The recessus inferior (*re. i*, figs. 22 C, 69; cf. figs. 71 C, 72 C) is developed ventrally to the crista intermedia and the lamina inferior. It is bounded by the septum nasi medially, by the lamina nariochoanalis laterally, and by the solum nasi ventrally. Through the fenestra nasobasalis it is anteriorly in communication with the cavum prenasale.

The posterior half of the nasal cavity has a small lateral recess (see p. 315) but is otherwise undivided. It is bounded by the septum nasi medially and by the postnasal wall posteriorly, its other walls being very imperfect. The solum nasi is developed only in its medial parts and it is thus represented only by a lamina along the ventral border of the septum nasi. The lateral parts of the solum nasi have become reduced by the strong development of the fenestra endochoanalis, which is large and laterally passes over without any boundary into a large opening, the fenestra nasolateralis, in the posterior parts of the lateral nasal wall and in the tectum nasi. On the dorsal side of the lamina-shaped solum nasi there is a long, rounded crest (*cr. em*, figs. 22 A, 27 B) running rostro-caudally and forming the support of the eminentia olfactoria.

The fenestra nasolateralis is in the main situated in the posterior parts of the lateral wall of the nasal cavity, behind and ventrally to the lamina obliqua and the lamina nariochoanalis, but it stretches also upwards into the tectum nasi where its foremost parts lie dorsally to the lamina obliqua. It is closed by the nasal bone (see fig. 69) and connective tissue and is traversed only by small nerves and vessels.

The fenestra endochoanalis (*fe. ench*, figs. 22 A, D, 23 B; cf. fig. 70 C) is bounded anteriorly and medially by the solum nasi and posteriorly


A
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la.Vo
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Fig. 23. *Rana esculenta.* Skeleton of the snout. *A*, in posterior, and *B*, in ventral view. Cartilage dotted. After a large specimen from Pilawa, Poland, in the possession of the Swedish Museum of Natural History. $^3/_1$.

Dpl, dermopalatine; *Enpt*, entopterygoid; *Fr-Pa*, fronto-parietal; *La*?, lachrymal or possibly a part of entopterygoid; Mx_1, Mx_2, Mx_3, pars dentalis, pars facialis, and pars palatina of maxillary; "*Na*", "nasal"; Pmx_1, Pmx_2, Pmx_3, pars dentalis, pars facialis and pars palatina of "premaxillary"; *Psph*, parasphenoid; *Set*, sphenethmoid; *Vo*, vomer; $c_{al}pal$, canal for antero-lateral terminal branch of r. palatinus VII; *cav. pren*, cavum prenasale; *cav. sbn*, cavum subnasale; $c_{m}pal$, canal for medial terminal branch of r. palatinus VII; *c. olf*, canalis olfactorius; *c. pr*, profundus canal; *cr. so*, crista supraorbitalis; *fe. ench*, fenestra endochoanalis; *fe. exch*, fenestra exochoanalis; *fe. pal*, anterior palatal fenestra; *la. Vo*, vertical tooth-bearing lamina of vomer; $pr_l Pmx_3$, $pr_m Pmx_3$, lateral and medial processes of the pars palatina of "premaxillary"; *pr. mxa*, *pr. mxp*, processus maxillaris anterior and posterior; *pr. pil*, processus prenasalis inferior lateralis; *s. olf*, median septum between canales olfactorii; *w. pn*, postnasal wall.

by the postnasal wall. Laterally it extends to the lateral wall of the nasal cavity, where, as already pointed out, it is continuous with the fenestra nasolateralis. Its lateral boundary is, therefore, very incomplete, consisting only of a short process, the processus maxillaris anterior (*pr. mxa*), from the antero-latero-ventral corner of the postnasal wall. The fenestra is partly closed ventrally by dermal bones (fig. 23 B) and by connective tissue. The fenestra exochoanalis (*fe. exch*, fig.

23 B) is situated underneath the posterior part of the fenestra endochoanalis. Its bounderies are largely incomplete.

The postnasal wall (*w. pn*, figs. 22 A, D, 23) occupies a practically transverse position between the nasal cavity and the orbit. In its medial ossified part it is pierced by the canalis olfactorius (*c. olf*) and dorsolaterally to this in the cartilaginous part of the wall by the profundus canal (*c. pr*, figs. 22 A, D, 23, 25 A, 30). The latter canal, which goes from the antero-dorso-medial corner of the orbit forwards to the nasal cavity, may be unbranching throughout its extent, but may also bifurcate into two branches, for the r. medialis and the r. lateralis narium of the n. profundus. When bifurcating within the postnasal wall it opens with two orifices in the nasal cavity. Close above its posterior (orbital) orifice there is a marked crest, the crista supraorbitalis of REINBACH's description (*cr. so*, figs. 22 A, 24, 69; cf. figs. 65 C, 67 C), which stretches some distance backwards along the foremost part of the dorso-lateral border of the interorbital wall. The ventro-lateral corner of the postnasal wall is expanded in a rostro-caudal direction and flattened from the sides and in lateral aspect appears as a triangular plate, the pars triangularis (*pr. tri*, figs. 22 A, D, 27 B; planum triangulare, GAUPP). Anteriorly the pars triangularis forms the processus maxillaris anterior (*pr. mxa*, fig. 22 A, D), already referred to above, whereas posteriorly it is continuous with the palatoquadrate by means of the processus maxillaris posterior (*pr. mxp*, figs. 22 A, D, 23). The pars triangularis is bent so that the anterior part of its medial face has a shallow rostro-caudal groove (fig. 27 B), the recessus lateralis of the nasal cavity (cf. p. 536), for the lateral diverticle of the nasal sac.

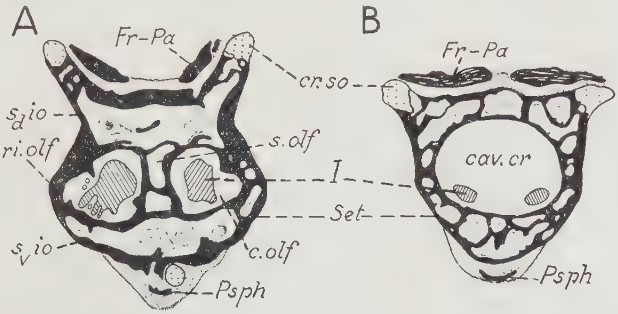


Fig. 24. Transverse sections through the anterior part of the orbitotemporal region. *A*, of *Rana cyanophlyctis* and, *B*, of *Rana hexadactyla*. From RAMASWAMI (1935, figs. 5 B and 5 D). Cartilage sparsely dotted.

Fr-Pa, fronto-parietal; *Psph*, parasphenoid; *Set*, sphenethmoid; *cav. cr*, cranial cavity; *c. olf*, canalis olfactorius; *cr. so.* crista supraorbitalis; *ri. olf*, olfactory ridge; *s. olf*, median septum between canales olfactorii; $s_d io$, dorsal part of interorbital wall; $s_v io$, ventral part of interorbital wall; *I*, n. olfactorius.

We shall now turn to other Anurans. The ethmoidal region in these is fundamentally as in *Rana*, though with certain differences (Hoffmann 1873—1878; Born 1876; W. K. Parker 1876; 1881; Peters 1882; Cope 1889; Sewertzoff 1891; Seydel 1895; v. Mihalkovics 1898; Bruner 1901; Gaupp 1905; Peeters 1910; McCotter 1917; Bolkay 1919; Higgins 1920; van Seters 1922; Lapage 1928 a; De Villiers 1929—1934 b; Schoonees 1930; Nemours 1930; C. A. Du Toit 1930; 1933; 1934; 1938; Noble 1931; Kruijtzer 1931; Yamada 1931 a; Du Toit and De Villiers 1932; Erdmann 1933; Kotthaus 1933; G. P. Du Toit 1933; D. S. Wagner 1934; Ramaswami 1934—1939; Kudo and Okutomi 1935; Stadtmüller 1936; De Beer 1937; Okutomi 1937; Pusey 1938; Reinbach 1939; Paterson 1939; 1939 a). Only the main differences that are of importance for a comparison with the Crossopterygians to be described below, will be mentioned here.

In certain forms, e. g. in *Scaphiopus* and *Megophrys* (Ramaswami 1935 a), the septum nasi is relatively broader than in *Rana*, and in several forms, inter alia in *Calyptocephalus* (fig. 22 E), the fenestra nasobasalis is strikingly small. In *Hyla* (Higgins 1920, pl. 6, figs. 38, 39), *Breviceps* (De Villiers 1931 c, p. 167), *Liopelma* (D. S. Wagner 1934, p. 66), *Alytes* etc. (Stadtmüller 1936, p. 557), a broad bridge of cartilage connects the lamina obliqua with the postnasal wall, dividing the fenestra nasolateralis into an upper part (cf. fig. 67 B, *fe. te*) completely surrounded by cartilage and a lower part passing over ventrally into the fenestra endochoanalis. In certain forms as in *Bombinator* and *Pelobates* (Born 1876; Gaupp 1905, p. 733; Stadtmüller 1936, p. 557) this cartilaginous bridge is present in the larvae only, whereas it is completely or almost completely reduced in the adults. In *Hyla* (Higgins 1920, p. 54; pl. 6, figs. 38, 39) the processus maxillaris anterior extends as far forwards as to be continuous with the lamina nariochoanalis, so that the fenestra nasolateralis and the fenestra endochoanalis are completely separated from one another. In all the forms mentioned the walls of the nasal cavity are thus more complete than in *Rana*.

Regarding the development of the crista intermedia, lamina superior, and lamina inferior certain differences of interest are also met with when comparing *Rana* with other Anurans. The crista intermedia is absent in *Arthroleptides* (C. A. Du Toit 1938, pp. 390—391). The lamina superior in both the form just mentioned and in *Calyptocephalus* (fig. 22 E; Reinbach 1939, p. 260) is fused along its anterior margin with the prenasal wall and for a short stretch also with the lateral wall of the nasal cavity. The lamina inferior is, as we have seen, in *Rana* connected with the lamina nariochoanalis somewhat ventrally to the ventral border of the fenestra endonarina communis. In certain other

Anurans, such as *Alytes* (STADTMÜLLER 1936, fig. 415 a), *Bombinator* (BORN 1876, pl. 40, fig. 20; BRUNER 1901, pl. 18, fig. 15; MÜLLER 1932, fig. 11), *Liopelma* (D. S. WAGNER 1934, fig. 1), and *Ascaphus* (DE VILLIERS 1934, fig. 3 A, B), on the other hand, the lamina inferior is continuous with the lamina nariochoanalis just along its dorsal margin and thus along the ventral border of the fenestra endonarina. In these forms, therefore, the part of the lateral wall of the nasal cavity that forms the lamina nariochoanalis bends medially, passing over directly into the lamina inferior. The lamina superior and inferior as well as the recessus medius are unusually small in *Ascaphus* (DE VILLIERS 1934, p. 10, fig. 3 A) and *Liopelma* (D. S. WAGNER 1934, p. 68). At any rate in the latter form the recessus inferior reaches further forwards than the recessus medius.

Besides in *Rana* the crista supraorbitalis has been met with in a great many other Anurans (*Rappia*, *Discoglossus*, *Xenophrys*, *Hylarana*, *Hyla*, *Alytes*, *Phyllomedusa*, *Calyptocephalus*, etc., W. K. PARKER 1881; REINBACH 1939). Laterally to this crest there is in *Alytes*, *Hyla*, and *Phyllomedusa* (W. K. PARKER 1881, pl. 24, figs. 1, 2; pl. 33, figs. 6, 7; pl. 34, figs. 7, 8; STADTMÜLLER 1931) an independent plate of cartilage, the "cartilago supraorbitalis" (cf. fig. 67 B, *cart. so*), which as pointed out by REINBACH (1939, p. 256) and as will also be shown below (p. 511) cannot be an independent lateral part of the crest itself. In *Rappia* an indistinct process pointing posteriorly (cf. figs. 65 B, 67 B, *pr. so*) is found on the dorsal margin of the postnasal wall just laterally to the supraorbital crest. As will be shown below (p. 511), this process may correspond to the ventro-lateral part of the lamina supraorbitalis in the Osteolepiform Crossopterygians (*la. so*, figs. 47, 65 A) whereas the "cartilago supraorbitalis" probably has its exact equivalent in the distal part of the processus supraorbitalis (*pr. sol*), which in certain forms (*Eusthenopteron foordi*) may be an independent element.

Finally, it is worthy of mention that the ethmoidal region in some Anurans may be much more extensively ossified than in *Rana*. This is the case for instance in *Anhydrophryne* (DE VILLIERS 1931 b, p. 334) and above all in *Hemisus* (DE VILLIERS 1931 a, p. 316). In the latter form not only the postnasal wall and the septum nasi are ossified, but also the parts of the tectum and solum nasi adjacent to the septum.

The septomaxillary (narial) in *Rana* (*Smx*, Smx_{am}, Smx_{pl}, figs. 27 A, 29, 69; cf. also figs. 68 C, 70 C, 71 C and 72 C; ECKER-WIEDERSHEIM-GAUPP 1896, p. 52, fig. 24; 1904, p. 648, figs. 139—142; BRUNER 1901, p. 338; pl. 17, fig. 9; pl. 18, figs. 11, 12, 14; LAPAGE 1928 a, p. 404, pl. 1, figs. 1, 3, 4; pl. 2, fig. 5; regarding the somewhat different shape in *Rana grayi* see C. A. DU TOIT 1933, pp. 720—721) is a small plate of bone roughly horseshoe-shaped and horizontal in position. The bone lies entirely within the nasal cavity, where it is found in the straight postero-lateral prolongation of the lamina superior and forms the roof of the postero-lateral part of the recessus medius. It consists of an antero-lateral part and two shanks pointing postero-medially, one antero-medial and one postero-lateral. The antero-medial shank (Smx_{am}) which is situated at a somewhat higher level than the postero-lateral one, is narrow and lies along and close to the free postero-lateral margin of the lamina superior. The postero-lateral shank (Smx_{pl}) is shorter and broader than the antero-medial one and abuts with its apex against the medial side of the pars terminalis somewhat above the transition to the lamina inferior. The antero-lateral part of the bone touches the dorsal margin of the lamina nariochoanalis laterally (in fig. 69, which shows a young stage, it is separated from the dorsal margin of the lamina nariochoanalis by a narrow slit; cf. Ecker-Wiedersheim-Gaupp 1896, fig. 24). Through the gap between the two shanks of the bone the recessus medius is in open communication with the recessus superior. The postero-lateral corner of the bone covers the groove *gr. dnl* (fig. 22 A, C) dorsally. Thus a short canal (*c. dnl*, fig. 68 C) is formed through which the nasolachrymal duct enters the postero-lateral part of the recessus medius.

Judging from the descriptions available the septomaxillary in other *Anura* seems in the main to be as in *Rana*, though with certain minor differences (Gaupp 1905; Lapage 1928 a; C. A. Du Toit 1930; 1933; 1934; 1938; Schoonees 1930; De Villiers 1929—1934 b; Du Toit and De Villiers 1932; G. P. Du Toit 1933; D. S. Wagner 1934; Ramaswami 1934; 1935; 1935 a; 1936; 1936 a, 1939, p. 48; Stadtmüller 1936, p. 624; Reinbach 1939; Paterson 1939; 1939 a). It is of interest to notice that in some forms, such as *Megophrys*, *Scaphiopus* (Ramaswami 1935 a, pp. 76—78), *Arthroleptides* (C. A. Du Toit 1938, p. 400), and *Calyptocephalus* (Reinbach 1939, p. 323) the bone has a small external lamina (cf. Smx_{fa}, figs. 68 B, 71 B). This external lamina which lies outside the nasal cavity is vertical and mainly rostro-caudal in extent. In this connection it is also worthy of mention that in larvae of *Calyptocephalus* the nasolachrymal duct enters the recessus medius dorsally to the septomaxillary, whereas in the adults of this form it has its entrance as is normally the case in Anurans, into the nasal cavity ventrally to the septomaxillary. During the embryonic development of *Calyptocephalus* it thus shifts downwards through the septomaxillary (Reinbach 1939, pp. 323—324).

As already demonstrated by Gaupp (1905, p. 746; cf. Watson 1917, p. 983) the septomaxillary of the *Anura* is a dermal bone. It has been established in a number of forms (see e. g. D. S. Wagner 1934, p. 71;

Stadtmüller 1936, p. 624; Ramaswami 1936 a, p. 1160; 1939, p. 49; Reinbach 1939, p. 323) to be separated from the adjacent cartilaginous parts of the nasal capsule by a layer of connective tissue. However this layer of connective tissue may sometimes be absent, a condition which caused Lapage (1928 a) to consider the septomaxillary a cartilage-bone. Since the layer of connective tissue in question is present in many forms (also in the larvae of *Calyptocephalus*; Reinbach 1939), its absence in some cases must obviously be secondary and due to reduction (cf. G. P. Du Toit 1933, p. 401; C. A. Du Toit 1934, p. 132). There are thus no reasons whatever for regarding the septomaxillary of the Anurans as a cartilage-bone (cf. p. 535).

As the corresponding skeletal element in Urodeles (cf. pp. 295—300), the palatoquadrate in Anurans has two different connections with the ethmoidal region, a medial larval one and a lateral definitive one (W. K. Parker 1871, 1876, 1881; Stöhr 1881; Sewertzoff 1891; Gaupp 1893; 1905; Spemann 1898; Peeters 1910; van Seters 1922; Kruijtzer 1931; Kotthaus 1933; Kudo and Okutomi 1935; Stadtmüller 1936; De Beer 1937; Okutomi 1937; Pusey 1938; Reinbach 1939; Paterson 1939; Imamura 1939). Regarding the development in later larval stages of the part of the palatoquadrate (the antero-medial process or commissura quadrato-cranialis anterior) that forms the larval connection and regarding the anterior extent of the palatoquadrate in adults there is a considerable disagreement between the opinion maintained by Gaupp and Pusey on the one hand, and that advanced by Reinbach on the other.

According to Gaupp (1893; 1905) and Pusey (1938; see also W. K. Parker 1871; Stöhr 1881; Spemann 1898; Peeters 1910) the development of the foremost part of the palatoquadrate in *Rana* takes place in the main as follows. Already in early embryonic stages (see Spemann 1898, fig. A; pl. 28, fig. 4; pl. 29, fig. 17) the antero-medial process of the palatoquadrate or commissura quadrato-cranialis anterior becomes confluent with the trabecula immediately ventrally to the place from which arises the embryonic postnasal wall, the lamina orbitonasalis. In the following stages the commissura quadrato-cranialis anterior (*com. qca*, fig. 25 A; cf. fig. 25 B) attains an almost transverse position and at the beginning of the metamorphosis it is situated so that its anterior margin is along and close below the ventral margin of the lamina orbitonasalis (*la. on*). From the lateral part of its anterior margin there arises a process, the processus quadrato-ethmoidalis (*pr. qe*; the antero-lateral process, see pp. 297, 299), which points in an antero-dorsal direction and which is connected with the foremost part of the trabecula by means of a ligament in front of the choana, the ligamentum quadrato-ethmoidale (*li. qe*). Another process arises from

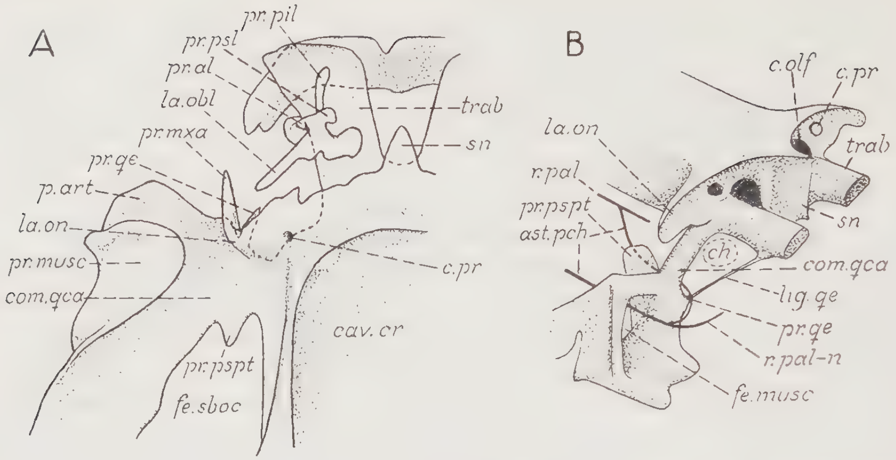


Fig. 25. *A. Rana fusca (temporaria).* Anterior part of endocranium and palatoquadrate of larva (stage 2, PUSEY). Dorsal view. From PUSEY (1938, pl. 39, fig. 17). *B. Calyptocephalus gayi.* Diagram of the anterior part of the palatoquadrate of the right side and adjacent parts of the endocranium, showing the course of certain nerves. Early larval stage (specimen *A* of REINBACH's description). Antero-lateral view. From REINBACH (1939, fig. 13 a) enlarged and slightly altered (cf. fig. 26 a below).

ast. pch, postchoanal anastomosis; *cav. cr,* cranial cavity; *ch,* position of choana; *c. olf,* canalis olfactorius; *com. qca,* commissura quadrato-cranialis anterior; *c. pr,* profundus canal; *fe. musc,* fenestra muscularis; *fe. sboc,* fenestra subocularis; *la. obl,* lamina obliqua; *la. on,* lamina orbitonasalis; *lig. qe,* ligamentum quadrato-ethmoidale; *p. art,* pars articularis quadrati; *pr. al,* processus alaris; *pr. musc,* processus muscularis; *pr. mxa,* processus maxillaris anterior; *pr. pil,* processus prenasalis inferior lateralis; *pr. psl,* processus prenasalis superior lateralis; *pr. pspt* processus pseudopterygoideus; *pr. qe,* processus quadrato-ethmoidalis; *r. pal,* r. palatinus VII; *r. pal-n,* r. palatonasalis; *sn,* septum nasi; *trab,* trabecula.

the posterior margin of the commissura. This process, the processus pseudopterygoideus (*pr. pspt*), which is formed by the lateral part of the posterior margin of the commissura, is broad and points in a postero-medial direction. The lamina orbitonasalis is at its lateral end provided with two processes, one directed anteriorly, which is the future processus maxillaris anterior (*pr. mxa*), and one directed postero-medially. The latter process, the processus maxillaris posterior (see GAUPP 1893, pl. 14, fig. 24; pl. 15, figs. 25, 26; PUSEY 1938, pl. 33, fig. 2), touches with the medial side of its apex the lateral side of the apex of the processus quadrato-ethmoidalis. In the following larval stages a fusion takes place between the processus quadrato-ethmoidalis and the processus maxillaris posterior. During the metamorphosis the commissura quadrato-cranialis anterior, the processus pseudopterygoideus, and the ligamentum quadrato-ethmoidale are said to disappear almost completely. Simultaneously with the disappearance of the structures mentioned the processus maxillaris posterior is said to increase considerably in length, pushing backwards the pars articularis (*p. art*) of the palatoquadrate, which in the larvae is situated far anteriorly. In the adults the processus maxillaris posterior (*pr. mxp*, figs. 22 A, 23 A) is assumed to represent approximately the anterior half of the bridge of cartilage, the palatoquadrate bar, that connects the pars articularis with the ventro-lateral corner (the pars triangularis) of the postnasal wall. As may thus be gathered, GAUPP and PUSEY hold the opinion that the palatoquadrate in the adult *Rana* does not extend forwards to the postnasal wall, but that it ends anteriorly almost opposite the middle of the orbit.

REINBACH (1939) has studied the embryonic development of *Calyptocephalus*. According to his observations the anterior part of the palatoquadrate in this form is in the main transformed in the following way during the metamorphosis. At the beginning of the metamorphosis the commissura quadrato-cranialis anterior is situated, as in *Rana*, with its anterior margin along and close below the ventral margin of the lamina orbitonasalis (planum antorbitale primarium, REINBACH). During the further progress of the metamorphosis the processus pseudopterygoideus is resorbed. The commissura quadrato-cranialis anterior, on the other hand, is largely retained and fuses with the lamina orbitonasalis, forming together with this the definitive postnasal wall (planum antorbitale secundarium s. definitivum, REINBACH). This wall in the adult *Calyptocephalus* includes, therefore, a palatoquadrate component. The processus maxillaris posterior is only a small "Knorpelzapfen" which fuses on its ventral side with the dorsal side of the processus quadrato-ethmoidalis (cf. below pp. 521—522). An increase in length of the antero-lateral parts of the palatoquadrate, but not of the processus maxillaris posterior, causes the pars articularis palatoquadrati to be pushed backwards. REINBACH thus arrives at the conclusion that in the adult *Calyptocephalus* the palatoquadrate forms the entire palatoquadrate bar and in addition also the ventral part of the postnasal wall.

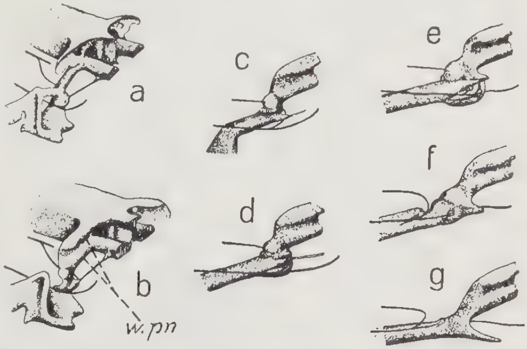


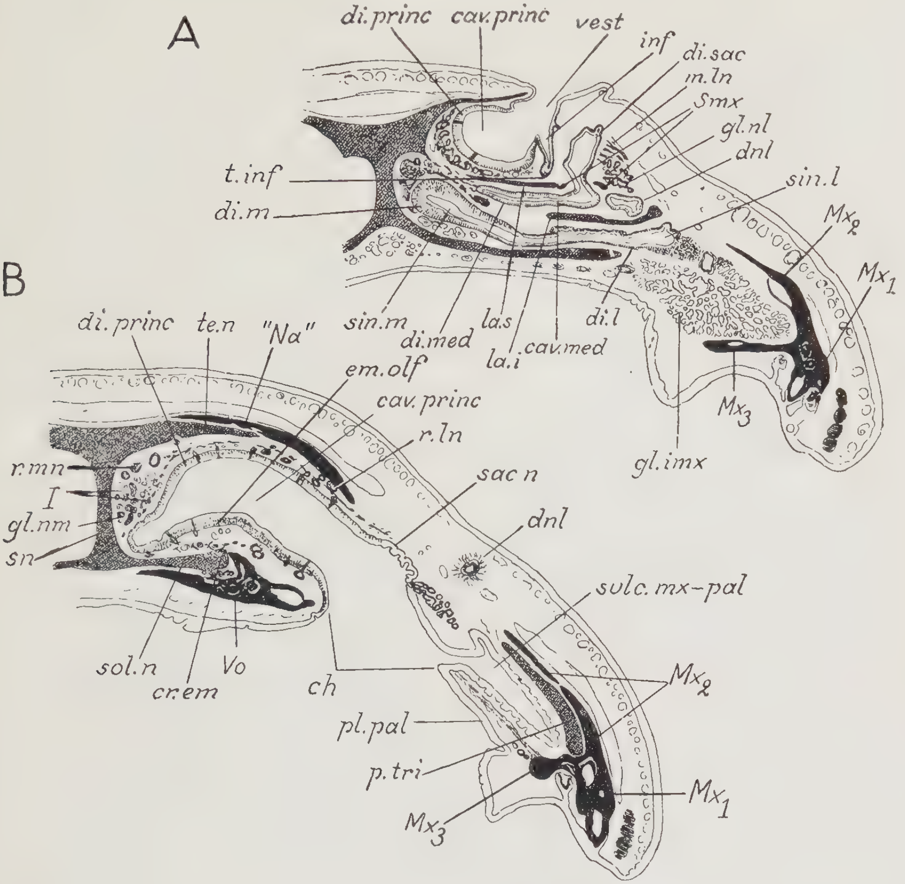
Fig. 26. *Calyptocephalus gayi.* Diagrams illustrating the embryonic development of the anterior end of the palatoquadrate in relation to the endocranium and certain nerves. Right side, oblique antero-lateral view. From REINBACH (1939, fig. 13).

w. pn, postnasal wall (planum antorbitale definitivum, REINBACH). For further explanations see fig. 25 B, which shows stage *a* somewhat enlarged and slightly altered.

If the observations made by GAUPP and PUSEY on the one hand and those made by REINBACH on the other were true, *Rana* and *Calyptocephalus* would differ considerably from each other with regard to the forward extent of the palatoquadrate and the transformation of the foremost part of this endoskeletal element. That this might be so is not quite out of the question, but the possibility must nevertheless be taken earnestly into consideration that either GAUPP and PUSEY or REINBACH may be mistaken in some way, and that the transformation of the anterior parts of the palatoquadrate in both the forms in question takes place in one and the same manner, as in Anurans in general. For palaeontological and other reasons, it is very likely, however, that REINBACH is right and that the palatoquadrate in Anurans in general during the metamorphosis is actually transformed essentially as described by him (cf. below pp. 520—525).

The intermaxillary gland in *Rana* (*gl. imx*, fig. 27 A) is strongly developed (WIEDERSHEIM 1876; ECKER-WIEDERSHEIM-GAUPP 1904, pp. 24—27; MÜLLER 1932, fig. 1; FAHRENHOLZ 1937, figs. 151—152). It occupies not only the cavum prenasale and cavum subnasale, but has also a paired intracapsular part which extends into the nasal cavity through the fenestra nasobasalis. Its intracapsular part together with another gland, the glandula nasalis medialis (*gl. nm*, figs. 27 B, 28 A, 30), lies close to the septum nasi between this and the nasal sac. The intermaxillary gland in *Rana* and in the majority of the Anurans (MÜLLER 1932; FAHRENHOLZ 1937) opens into the roof of the mouth through several ducts (*gl. imxd*, fig. 31). However, in *Arthroleptides* (C. A. DU TOIT 1938, pp. 394—397) the efferent ducts unite into a single one, the orifice of which is situated between the choanae, a condition which is regarded by DU TOIT as possibly primitive (cf. p. 506). FAHRENHOLZ (1937, pp. 118—119), on the other hand, holds a reverse opinion, maintaining that the presence of several efferent ducts is a primitive condition. An intermaxillary gland with one efferent duct (glandula monostomatica) must, therefore, according to him have arisen from one with numerous efferent ducts (glandula polystomatica) by a concentration and fusion of several primary efferent ducts. The earlier embryonic development of the intermaxillary gland in Anurans is very imperfectly known. The gland is said by OEDER (1906) to arise in *Rana* from an unpaired primordium, but in *Bufo* from a paired primordium, and this statement by OEDER has recently, as regards *Bufo*, been corroborated by RIECK (1932; cf. FUKUCHI 1934). According to PATERSON (1939 a, p. 395) the intermaxillary gland in *Xenopus* is paired.

The nasal sac in *Rana* (*sac n*, figs. 27, 28 A, 30, cf. figs. 28 B and 72 C) is of a much more complicated shape than in the Gnathostome Vertebrates dealt with above in this work (BORN 1876; SEYDEL 1895; HINSBERG 1901; PETER 1901; ECKER-WIEDERSHEIM-GAUPP 1904; MCCOTTER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sol.n
Vo
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Fig. 27. *Rana esculenta.* Transverse sections through the snout of a young individual. *A,* through the external nostril, and, *B,* through the choana. $^{14}/_{1}$. From ECKER-WIEDERSHEIM-GAUPP (1904, figs. 140 and 145).

Mx$_1$, *Mx*$_2$, *Mx*$_3$, pars dentalis, pars facialis, and pars palatina of the maxillary; "*Na*", "nasal"; *Smx,* septomaxillary; *Vo,* vomer; *cav. med, cav. princ,* cavum medium and cavum principale of the cavity of the nasal sac; *ch,* choana; *cr. em,* crest on dorsal face of solum nasi, supporting the eminentia olfactoria; *di. l, di.m,* diverticulum laterale and diverticulum mediale of diverticulum inferius; *di. med, di. princ,* diverticulum medium and diverticulum principale; *di. sac,* diverticulum sacciformis; *dnl,* ductus nasolacrimalis; *em. olf,* eminentia olfactoria; *gl. imx,* glandula intermaxillaris; *gl. nl, gl. nm,* glandula nasalis lateralis and medialis; *inf,* infundibulum; *la. i,* lamina inferior; *la. s,* lamina superior; *m. ln,* m. lateralis narium; *pl. pal,* plica palatina; *p. tri,* pars triangularis of postnasal wall; *r. ln,* r. lateralis narium of n. profundus; *r. mn,* r. medialis narium of n. profundus; *sac n,* nasal sac; *sin. l,* sinus lateralis; *sin. m,* sinus medialis; *sn,* septum nasi; *sol. n,* solum nasi; *sulc. mx-pal,* sulcus maxillo-palatinus; *te. n,* tectum nasi; *t. inf,* tuba infundibuli; *vest,* vestibulum; *I,* n. olfactorius.

1917; C. A. DU TOIT 1933; HELLING 1938). It is differentiated into three main divisions, an upper, a middle, and a lower one. The cavities of these divisions are generally described as the cavum principale, cavum medium, and cavum inferius, respectively; the three divisions themselves may here be referred to as the diverticulum principale, diverticulum medium, and diverticulum inferius, respectively.

The diverticulum principale (*di.princ*, figs. 27, 28 A; cf. fig. 28 B) forms the main part of the nasal sac and it is also the division of the nasal sac from which issue both the internal (*cht*) and the anterior, external nasal tubes. Its anterior part is bulged out into a blind pouch, the saccus superior (*di. s*; oberer Blindsack, Born) which occupies the anterior parts of the recessus superior of the nasal cavity. The portion of the cavum principale that is situated nearest to the external nasal tube is partly bounded off as a cavity of its own, the vestibulum (*vest*). The cavum principale is in communication with the cavum medium and the cavum inferius by a fairly narrow cavity, the infundibulum (*inf*). The part of the nasal sac surrounding the infundibulum may be termed the tuba infundibuli (*t. inf*). The tuba infundibuli as thus defined is somewhat compressed in a mainly rostro-caudal direction. It passes downwards from the diverticulum principale through the gap between the two shanks of the septomaxillary.

The diverticulum medium (*di. med*, figs. 27 A, 28 A; cf. figs. 28 B, 72 B) which is the smallest of the main divisions of the nasal sac, is situated in the recessus medius of the nasal cavity. From the postero-lateral part of this diverticle issues the nasolachrymal duct (posterior external nasal tube) which, as has already been pointed out, leaves the nasal cavity ventrally to the postero-lateral corner of the septomaxillary through a short canal (*c. dnl*, fig. 68 C, cf. fig. 29). The secretion of the nasolachrymal duct is not discharged through the cavum medium and the infundibulum, but is passed directly to the external nostril through a special fold, by Helling (1938, pp. 633, 637) called the "Schaltstück" ("*Sst*", fig. 28 A), which passes through the most lateral part of the gap between the two shanks of the septomaxillary (cf. fig. 29). The "Schaltstück" may be more or less completely separated from the tuba infundibuli and the postero-lateral part of the diverticulum medium. In *Rana fusca* the "Schaltstück" is throughout its extent in connection with the tuba infundibuli (fig. 28 A), whereas in *R. esculenta* Helling (1938, p. 637) states that its dorsal part is completely separated from the tuba infundibuli.

The diverticulum inferius (*di. i*, fig. 28 A; cf. fig. 72 C) is composed of two subsections, the diverticulum mediale and the diverticulum laterale. The diverticulum mediale or Jacobson's organ (*di. m*, figs. 27 A, 28 A; cf. fig. 28 B) occupies the antero-ventro-medial part of the nasal cavity. Its foremost part lies underneath the crista intermedia, that is to say in the recessus inferior. Medially it extends to the septum nasi. The diverticulum laterale (*di. l*, figs. 27 A, 28 A; cf. fig. 28 B) is situated in the postero-ventro-lateral part of the nasal cavity. It forms a groove, the sinus lateralis nasi (*sin. l*; seitliche Nasenrinne; SEYDEL; recessus lateralis; GAUPP). Laterally to the choana it passes over backwards into the sulcus maxillo-palatinus (*sulc.mx-pal*, fig. 27 B) which is bounded ventrally by a fold of the mucous membrane of the roof of the mouth, the plica palatina (*pl. pal*, fig. 27 B; see also ECKER-WIEDERSHEIM-GAUPP 1904, figs. 6, 7 a, 12; BENDER 1907, pl. 24, fig. 8). Since there is no homologue of SEYDEL's palatal process in the Urodeles, the plica palatina is not supported by any skeletal formation. As has already been mentioned the diverticulum laterale is situated medially to the anterior part of the pars triangularis of the postnasal wall.

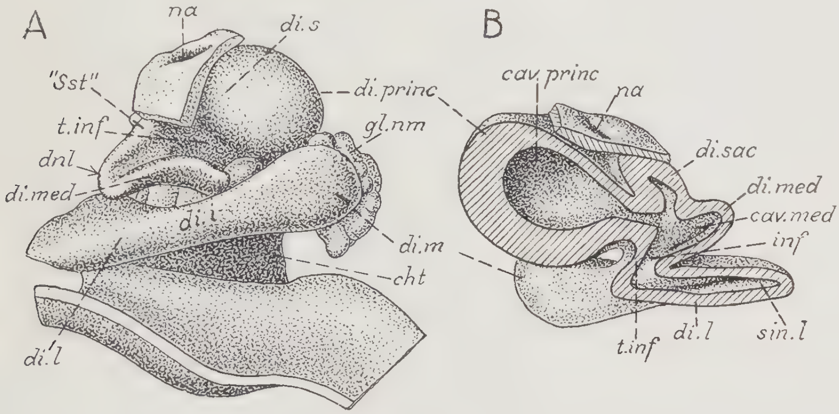

Fig. 28. *A. Rana fusca.* Right nasal sac of larva in metamorphosis. Anterior view. $^{50}/_{1}$. From HINSBERG (1901, pl. 21, fig. 21). *B. Alytes obstetricans.* Anterior half of right nasal sac of young animal after metamorphosis. Postero-dorsal view. $^{50}/_{1}$. From ROWEDDER (1937, fig. 14).

"Sst", "Schaltstück" of HELLING's description; *cav. med, cav. princ*, cavum medium and cavum principale, of cavity of nasal sac; *cht*, choanal tube; *di. i*, diverticulum inferius of nasal sac; *di. l, di. m*, diverticulum laterale and mediale (subsections of diverticulum inferius); *di. med, di. princ*, diverticulum medium and principale of nasal sac; *di. s*, saccus superior; *di. sac*, diverticulum sacciformis; *dnl*, arrow indicating the place where the nasolachrymal duct leaves the nasal sac; *gl. nm*, glandula nasalis medialis; *inf*, infundibulum; *na*, external nostril; *sin. l*, sinus lateralis; *t. inf*, tuba infundibuli.

In the *Anura Phaneroglossa* in general the nasal sac is in its essential characters as in *Rana* (DE VILLIERS 1929—1934 b; C. A. DU TOIT 1930; 1934; 1938; YAMADA 1931; G. P. DU TOIT 1933; RAMASWAMI 1934; 1935; 1935 a; 1936; 1936 a; D. S. WAGNER 1934; MATTHES 1934; FUKUCHI 1936; WATANABE 1936; ROWEDDER 1937; HELLING 1938). In the *Anura Aglossa* it is also in *Xenopus* (FÖSKE 1934; PATERSON 1939; 1939 a) mainly as in *Rana*, whereas in *Pipa* (TRAHMS 1936) it presents in some respects a different structure, resembling that in Urodeles. In the following I shall comment upon the position of Jacobson's organ (diverticulum mediale) in various forms and upon the structures included by Föske and Helling under the title "Die Mündungszone des Tränennasenganges", thus the part of the nasal sac through which the secretion of the nasolachrymal duct is transferred to the vestibulum.

Jacobson's organ (diverticulum mediale) in Anurans in general has a fairly varying position. In certain forms, such as *Bombinator* and *Xenopus* (Helling 1938, p. 624), it is connected with the lateral part of the diverticulum principale, extending from this connection forwards or (*Xenopus*) forwards and medially. In the majority of forms, however, it is connected with the middle part of the diverticulum principale and has a varying extent in an anterior and medial direction. In several forms it goes farther medially than the overlying part of the diverticulum principale and may as in *Megalixalus* be curved upwards between the said part of the diverticulum principale and the septum nasi. Helling regards its lateral position as primitive, maintaining that during the phyletic development the organ migrated medially in the nasal civity. It deserves to be emphasized, however, that in *Xenopus*, where, as just pointed out, it is connected with the lateral part of the diverticulum principale, the organ in question arises as in other Anurans as a bulge from the anterior part of the nasal sac. As will be demonstrated below (p. 536) it was probably situated ventro-medially to the main part of the nasal sac in the piscine ancestors of the Anurans.

Regarding the "Mündungszone" of the nasolachrymal duct, varying conditions are met with in Anurans. A condition common to the majority of Anurans is that the duct in question opens into the cavum medium and that from the diverticulum medium a connection (the "Schaltstück"), more or less independent, leads up to the vestibulum. In certain forms, as in *Xenopus* and *Crinia*, however, the duct does not open into the cavum medium. In *Xenopus* (Föske 1934; Paterson 1939 a) it goes to a special bulge of the diverticulum principale connected with the vestibulum, a bulge which, as shown by Helling, cannot be homologized to any part of the diverticulum medium in the Anurans. In *Crinia* (C. A. Du Toit 1934) the duct goes to a lateral bulge of the tuba infundibuli that is situated dorsally to the diverticulum medium. In both *Xenopus* and *Crinia*, however, the nasal sac has a very complicated shape, indicating that it is highly specialized. In this connection *Ascaphus* is of particular interest. By several writers it is regarded as one of the most primitive forms among recent Anurans. As has already been mentioned, the recessus medius of the nasal capsule is unusually small in this form (see p. 317), and accordingly the diverticulum medium is also small. The "Schaltstück" is absent and the only communication between the cavum medium and the vestibulum is thus formed by the infundibulum. The nasolachrymal duct opens into the infundibulum at the transition to the cavum medium. Consequently the secretion of the nasolachrymal duct is in *Ascaphus* discharged into the vestibulum through the infundibulum.

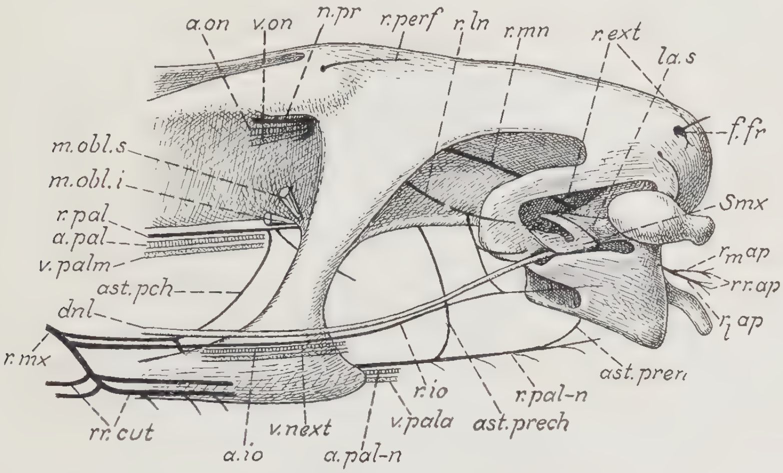

Fig. 29. *Rana esculenta.* Diagram showing the ductus nasolacrimalis, the oblique eye-muscles, the nerves, and the main vessels of the snout, in their relation to the endocranium. The septomaxillary in position. Lateral view. Compilation after ECKER-WIEDERSHEIM-GAUPP (1899; 1904), but the septomaxillary slightly altered in accordance with figure given by LAPAGE (1928 a, pl. 1, fig. 1) of the septomaxillary in *R. fusca* (*temporaria*).

Smx, septomaxillary; *a. io*, a. infraorbitalis; *a. on*, a. orbitonasalis; *a. pal*, a. palatina; *a. pal-n*, a. palatonasalis; *ast. pch, ast. prech, ast. pren*, postchoanal, prechoanal and prenasal nerve anastomosis; *dnl*, ductus nasolacrimalis; *f. fr*, foramen frontale; *la. s*, lamina superior; *m. obl. i*, m. obliquus inferior; *m. obl. s*, m. obliquus superior; *n. pr*, n. profundus; *r. ext*, r. externus narium of n. profundus; *r. io*, r. infraorbitalis of r. maxillaris V; $r_l ap$, $r_m ap$, lateral and medial terminal branches of r. medialis narium; *r. ln*, r. lateralis narium of n. profundus; *r. mn*, r. medialis narium of n. profundus; *r. mx*, r. maxillaris V; *r. pal*, r. palatinus VII; *r. pal-n*, r. palatonasalis; *r. perf*, r. frontalis perforans of n. profundus; *rr. ap*, rami apicales; *rr. cut*, rami cutanei maxillares; *v. next*, v. nasalis externa; *v. on*, v. orbitonasalis; *v. pala*, v. palatina anterior; *v. palm*, v. palatina medialis.

The brain and the olfactory nerves are fairly completely described in *Rana* (ECKER-WIEDERSHEIM-GAUPP 1899, pp. 22—128, figs. 4—8; PLATE 1922, fig. 523) whereas they are imperfectly known in other Anurans. The hemispheres of the forebrain (*hem*, fig. 30) are ovoid and somewhat tapering forwards. They are separated in their anterior parts by a narrow median slit (fissura sagittalis). The bulbi olfactorii (*b. olf*) are situated straight in front of and close to the hemispheres, the external boundary being indicated only by a shallow transverse groove. They are comparatively long and fused with each other medially so as to pass over into one another without any distinct external demarcation. The olfactory nerve (*I*) of either side arises from two roots, a posterior (lateral) one, emerging from the antero-ventro-lateral part of the hemisphere, and a considerably stronger anterior (medial) one, which leaves the anterior ventral part of the bulbus olfactorius. The brain does not reach the anterior end of the cranial cavity. Before entering the canalis olfactorius the olfactory nerves thus traverse the foremost part of the cranial cavity (figs. 24 B, 30).

The n. profundus (*n. pr*, figs. 29, 30) in *Rana* (Ecker-Wiedersheim-Gaupp 1899, pp. 133—137) traverses the orbit dorsally to the n. opticus and the oblique muscles of the eye, reaching the nasal cavity through the profundus canal already described. While still in the orbit it gives off a few dorsal branches, the rr. frontales et palpebrales superiores anteriores, the anterior of which (*rr. fra*, fig. 30) are distributed to the skin on the postero-dorso-lateral parts of the snout as far forwards as to the external nostril. In the profundus canal a fine branch, the r. frontalis perforans (*r. perf*, figs. 29, 30), ascends from the nerve to the dorsal side of the snout, through a fine canal of its own (cf. fig. 67 *c. perf*). This branch supplies the skin near the median line. Anteriorly to or, sometimes, slightly behind the origin of the fine branch just described the n. profundus bifurcates into a lateral and a medial nasal branch. This bifurcation may take place either in front of or within the profundus canal. In the latter case the profundus canal is often subdivided anteriorly into two branches opening independently of one another into the nasal cavity. The lateral nasal branch, the r. lateralis narium (*r. ln*, figs. 27 B, 29, 30), goes forwards and laterally to an area somewhat postero-latero-ventrally to the external nostril, there breaking up into a few twigs one of which anastomoses with the r. infraorbitalis of the r. maxillaris V. The medial nasal branch, the r. medialis narium (*r. mn*), is stronger than the r. lateralis narium. It passes first anteriorly and somewhat medially above the n. olfactorius and the glandula nasalis medialis, gradually approaching the septum nasi. Then it takes a course more straight forwards and somewhat downwards, passing underneath the crista intermedia through the medial part of the recessus inferior. It leaves the nasal cavity through the fenestra nasobasalis, thence continuing into the cavum prenasale. Here it goes between the tubes of the intermaxillary gland dividing into a fine medial ($r_m ap$, figs. 29, 30) and a stronger lateral branch ($r_l ap$). These branches in their turn break up into fine twigs (*rr. ap*; rr. apicales) which supply the skin on the tip of the snout. Slightly before its entrance into the recessus inferior, immediately behind the crista intermedia, the r. medialis narium sends out a dorsal branch, the r. externus narium (*r. ext*, figs. 29, 30), which ascends through the foramen frontale in the tectum nasi and which is distributed to the skin medially to the external nostril. In or somewhat behind the fenestra nasobasalis there issues a ventral branch from the r. medialis narium. In the cavum prenasale this ventral branch (*$r_v$mn*, fig. 30) bends almost straight downwards, joining the medial terminal branch of the r. palatinus VII and forming the prenasal anastomosis (*ast. pren*, figs. 29, 31; r. communicans c. N. palatino, Gaupp). From this anastomosis there issue fine branches (*rr. Pmx*$_3$, fig. 31; cf. Stirling and MacDonald 1883, pl. 13, fig. 1) to the part of the mucous membrane of the palate that lines the pars palatina (*Pmx*$_3$) of the "premaxillary".

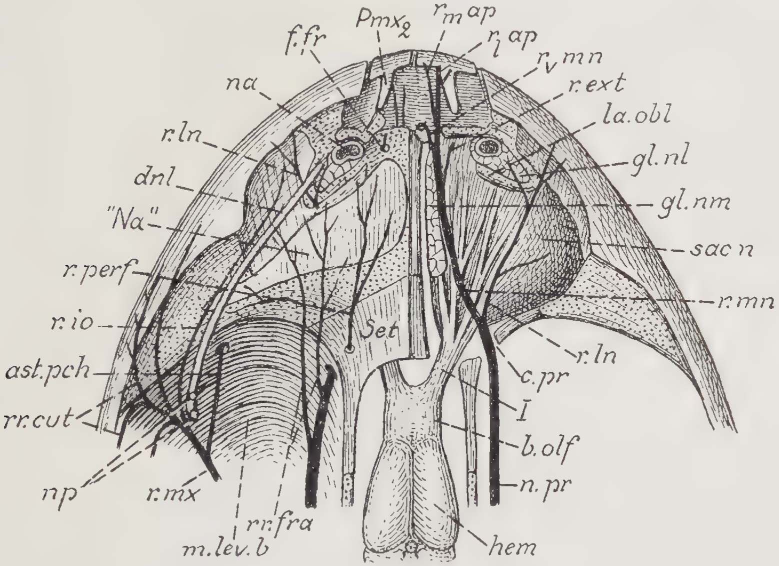

Fig. 30. *Rana esculenta.* Diagram showing the forebrain and the nerves of the snout in their relation to the skeleton and certain soft parts. Dorsal view. Compilation from Ecker-Wiedersheim-Gaupp (1899). Cartilage dotted.

"Na" "nasal"; *Pmx*$_2$, pars facialis of "premaxillary"; *Set*, sphenethmoid; *ast. pch*, postchoanal nerve anastomosis; *b. olf*, bulbus olfactorius; *c. pr*, profundus canal; *dnl*, ductus nasolacrimalis; *f. fr*, foramen frontale; *gl. nl*, *gl. nm*, glandula nasalis lateralis and medialis, resp.; *hem*, hemisphere of forebrain; *la. obl*, lamina obliqua; *m. lev. b*, m. levator bulbi; *na*, anterior external nostril; *np*, posterior apertures of ductus nasolacrimalis (posterior external nostrils); *n. pr*, n. profundus; *r. ext*, r. externus narium of n. profundus; *r. io*, r. infraorbitalis; *$r_l$ap*, *$r_m$ap*, lateral and medial terminal branch of r. medialis narium; *r. ln*, r. lateralis narium of n. profundus; *r. mn*, r. medialis narium of n. profundus; *r. mx*, r. maxillaris V; *r. perf*, r. frontalis perforans of n. profundus; *rr. cut*, rr. cutanei maxillares; *rr. fra*, rr. frontales anteriores of n. profundus; *$r_v$mn*, ventral terminal branch of r. medialis narium; *sac n*, nasal sac; *I*, n. olfactorius.

The r. maxillaris V (*r. mx*, figs. 29, 30) in Rana (Ecker-Wieders-

HEIM-GAUPP 1899, pp. 139—140) is far more strongly developed than the corresponding nerve in Urodeles. It reaches far forwards in front of the orbit and supplies the whole lateral part of the snout. In the middle part of the orbit it sends off two large branches, the postchoanal anastomosis (r. communicans c. N. palatino, GAUPP) and the r. infraorbitalis, both of which go to the snout. The remainder of the nerve turns somewhat laterally and downwards and after piercing a membrane of connective tissue between the maxillary and the lower side of the eye bulb it breaks up into branches running both posteriorly and anteriorly, the rr. cutanei maxillares (*rr. cut*), which are distributed to the skin outside the maxillary. The postchoanal anastomosis (*ast. pch*, figs. 29—31; cf. figs. 25 B, 26) first runs forwards through the orbit dorsally both to the musculus levator bulbi (*m. lev. b*) and the tendinous membrane forming the anterior continuation of that muscle. It then pierces the membrane just referred to and traversing the fenestra subocularis it curves medially and downwards, finally to anastomose with the r. palatinus VII. The passage of the postchoanal anastomosis as here described refers to the conditions in the adults. In the larvae the anastomosis crosses the palatoquadrate bar on the lateral side and not, as in the adults, on the medial side (cf. pp. 332—333). The r. infraorbitalis (*r. io*) goes forwards through the ventro-lateral part of the orbit, thence continuing forwards laterally to the lower part of the lateral side of the ethmoidal region and the nasal bone. It is traceable as far forwards as to the vicinity of the external nostril. In its passage forwards it lies close to the nasolachrymal duct and is accompanied by two vessels, an artery and a vein.

The r. palatinus VII (*r. pal*, figs. 29, 31) passes forwards fairly close to the lateral margin of the parasphenoid (STIRLING and MACDONALD 1883; ECKER-WIEDERSHEIM-GAUPP 1899, pp. 143—146; cf. *Rana mugiens*, BENDER 1907, pl. 24, fig. 8). Below the posterior margin of the dermopalatine it gives off lateral branches which join each other behind the choana and pass over into the postchoanal anastomosis. From the lateral part of this anastomosis there issues a branch, the r. palatonasalis (*r. pal-n*, figs. 29, 31), which has the appearance of an anterior continuation of the part of the anastomosis formed by the r. maxillaris V and which, therefore, probably mainly is a trigeminus branch. After giving off a few lateral branches running posteriorly, the r. palatonasalis crosses the ventro-lateral part of the postnasal wall below the dermopalatine, distributing several branches to the mucous membrane lining the pars palatina of the maxillary. Here it runs forwards laterally to the choana and is situated in the basal part of the plica palatina. Thence it continues forwards ventrally to the lateral part of the nasal sac and ventrally also to the anterior part of the solum nasi whence it enters the cavum subnasale. In this cavity it forms an anastomosis, the prechoanal anastomosis (*ast. prech*, figs. 29, 31), with the antero-lateral terminal branch of the r. palatinus VII. Though not actually stated by ECKER-WIEDERSHEIM-GAUPP, it is conceivable that r. palatonasalis supplies the teeth of the maxillary, "premaxillary", and vomer.

In front of the postchoanal anastomosis the r. palatinus VII goes dorsally to the posterior part of the vomer of its side, pierces the anterior part of the vomer, and bifurcates into two terminal branches, an antero-lateral and a medial one. The former of these branches ($r_{al}pal$; r. communicans c. N. palato-nasali, GAUPP) which usually emerges from the vomer through a foramen of its own ($c_{al}pal$, fig. 23 B), gives off a fine lateral twig (r_lpal, fig. 31) after which it connects with the r. palatonasalis forming with this the prechoanal anastomosis already referred to. The medial terminal branch (r_mpal, fig. 31; r. intermaxillaris s. communicans c. N. ophthalmico GAUPP) forms with the ventral terminal branch (r_vmn) of the r. medialis narium of the n. profundus the prenasal anastomosis (*ast. pren*) described above.

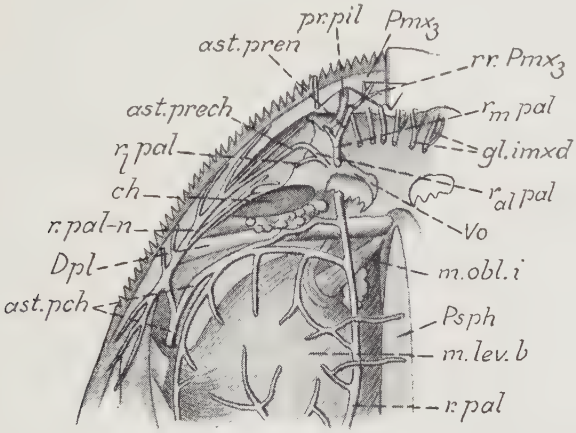

Fig. 31. *Rana esculenta.* Diagram showing the nerves of the snout in their relation to the skeleton and certain soft parts. Right side in ventral aspect. From ECKER-WIEDERSHEIM-GAUPP (1899, fig. 39), slightly altered.

Dpl, dermopalatine; Pmx_3, pars palatina of "premaxillary"; *Psph*, parasphenoid; *Vo*, vomer; *ast. pch, ast. prech, ast. pren,* postchoanal, prechoanal and prenasal nerve anastomoses; *ch*, choana; *gl. imxd*, ducts of intermaxillary gland; *m. lev. b*, m. levator bulbi; *m. obl. i*, m. obliquus inferior; *pr. pil*, processus prenasalis inferior lateralis; $r_{al}pal$, r_lpal, r_mpal, antero-lateral, lateral, and medial terminal branches of r. palatinus VII; *r. pal*, r. palatinus VII; *r. pal-n*, r. palatonasalis; *rr.* Pmx_3, branches of prenasal anastomosis supplying the mucous membrane of the pars palatina of "premaxillary".

In the larvae the r. ophthalmicus lateralis and the r. buccalis lateralis are both present (STRONG 1895; ESCHER 1925). When leaving the orbit the r. ophthalmicus lateralis lies laterally to the n. profundus (cf. Strong 1895, pl. 12, fig. A). In the connective tissue on the dorsal side of the snout it goes first antero-medially thence somewhat anteriorly to the external nostril, curving antero-laterally. The r. buccalis lateralis passes forwards in the upper lip, but does not seem to join any of the branches of the r. maxillaris V.

As may be gathered from this account of the nerves in *Rana*, there are at least four paired nerve anastomoses in the snout of this form, viz:

1) a postchoanal anastomosis (*ast. pch*) between the r. maxillaris V and the r. palatinus VII;
2) a prechoanal anastomosis (*ast. prech*) between the r. palatonasalis and the antero-lateral terminal branch of the r. palatinus VII;
3) a prenasal anastomosis (*ast. pren*) between the r. medialis narium of the n. profundus and the medial terminal branch of the r. palatinus VII; and finally
4) an anastomosis between the r. lateralis narium of the n. profundus and the r. infraorbitalis V.

Besides in *Rana* the course of the nerves of the snout has been described in the *Anura Phaneroglossa* in *Calyptocephalus* only (Reinbach 1939, pp. 256—265, 278—281), in which, as far as it is known, it seems to be very much as in *Rana*. In the *Anura Aglossa* it is different, resembling to some extent the course of the nerves in Urodeles (Grönberg 1894; Arnold 1894; Kotthaus 1933; Paterson 1939).

The position of the postchoanal anastomosis and of the r. palatonasalis in relation to the foremost part of the palatoquadrate during the larval development is of a certain interest. The changes in the course of the said two nerves that take place in connection with the transformation of the anterior part of the palatoquadrate has been described by Gaupp (1893) in *Rana*, and recently by Reinbach (1939, pp. 278—281, fig. 13) in *Calyptocephalus*. Since the latter description is the more detailed one, the changes in question are easier to understand in *Calyptocephalus* than in *Rana*. The subsequent brief review of them therefore refers only to the conditions in *Calyptocephalus*. In this form (figs. 25 B, 26) the postchoanal anastomosis (*ast. pch*) in early larval stages traverses the so-called fenestra muscularis (*fe. musc*). After giving off the r. palatonasalis (*r. pal-n*) it curves medially, ventrally and backwards, then passing over into the r. palatinus VII. During this part of its course it crosses first the dorsal side of the most lateral part of the commissura quadrato-cranialis anterior (*com. qca*) immediately laterally to the base of the processus quadrato-ethmoidalis (*pr. qe*) and then bends round the anterior margin of the commissura. According to Reinbach the commissura fuses with the ventral margin of the lamina orbitonasalis (*la. on*) in later larval stages, forming together with this, as has already been mentioned (p. 321), the definitive postnasal wall (*w. pn*, fig. 26 b; planum antorbitale definitivum, REINBACH). A new formation of cartilage then causes both the postchoanal anastomosis and the r. palatonasalis to be enclosed in canals in the antero-lateral part of the palatoquadrate (fig. 26 e). By resorption of the cartilage posteriorly to its canal the postchoanal anastomosis gradually appears to sink down through the palatoquadrate bar and finally passes entirely posteriorly and medially to it. During the larval period it thus "migrates" through the palatoquadrate bar and in the adults it passes entirely behind and medially to this skeletal element. A similar "migration" though in a medioventral direction can also be established for the r. palatonasalis. In recently metamorphosed individuals, however, this nerve is still enclosed in a canal (fig. 26 g).

The main vessels of the snout in *Rana* (fig. 29) accompany the nerves. With the exception of the lateralis branches all the main nerves are thus accompained by both an artery and a vein (ECKER WIEDERSHEIM-GAUPP 1899). There is an a. orbitonasalis (*a. on*) and a v. orbitonasalis (*v. on*) which both together with the n. profundus traverse the profundus canal and which both divide into a medial and a lateral nasal branch accompanying the medial and lateral nasal branches of the n. profundus. The a. maxillaris is strongly developed and breaks up into three main branches, the aa. cutanei maxillares, the a. infraorbitalis (*a. io*), and the postchoanal arterial anastomosis (r. communicans c. A. palatino, GAUPP), of which the latter gives off an a. palatonasalis (*a. pal-n*). All these branches of the a. maxillaris accompany the correspondingly termed branches of the r. maxillaris V. The lateral parts of the snout are drained by the vv. cutanei maxillares, the v. nasalis externa (*v. next*), and the v. palatina anterior. Of these the v. nasalis externa accompanies the a. infraorbitalis, whereas the v. palatina anterior accompanies the a. palatonasalis and the postchoanal arterial anastomosis. The medial part of the palate is supplied with blood through the a. palatina (*a. pal*) which together with the r. palatinus VII pierces the vomer, in which, as that nerve, it bifurcates into a medial and an antero-lateral branch. The blood of the palate is received by the v. palatina medialis (*v. palm*). The v. cerebralis anterior is absent in the adult frog, but as shown by VAN GELDEREN (1924, pp. 572—576) it is present in young larvae of both *Rana* and *Alytes*. It arises from the posterior parts of the forebrain and pierces the lateral wall of the cranial cavity, in these young stages consisting of connective tissue only, in the region medially to the eye bulb.

IV. The snout in Crossopterygians.

For reasons mentioned in the Preface the snout in Crossopterygians cannot be exhaustively treated in this work. Its endocranial parts are described in full, while its sensory canals and dermal bones have been dealt with more superficially. The sensory canals have thus been treated in their broader features only. Their nerve supply, their tubes and pores, and other details in their development have not been entered upon. As regards the dermal bones I have confined myself to describe in detail only those of particular interest to comparative anatomy.

A. Sensory canals and dermal bones.

Before proceeding to a detailed account of the snout in the various groups of Crossopterygians, I shall comment upon the sensory canals and dermal bones of the snout in Crossopterygians in general. At the same time I shall also undertake a revision of the terms that have been used by NIELSEN (1936) and J. L. B. SMITH (1939) to designate the sensory canals and dermal bones of the snout in the Coelacanthids.

The supraorbital sensory canal (*soc*, figs. 32—37, 41, 46 A, 52 B, 53, 58; pl. 6, fig. 1; pl. 7, fig. 2; pl. 8, fig. 1; pl. 9, fig. 1; pls. 11—13; cf. figs. 43, 47; pl. 14; pl. 15, fig. 2, *gr. soc*, *socp*) in all three main groups of Crossopterygians lies on the dorsal side of the snout and forms a more or less pronounced S-shaped bend. The canal passes dorso-medially to the external nostrils and anastomoses anteriorly with the infraorbital canal of its side antero-medially to the anterior external nostril.

In the hindmost part of the snout the infraorbital sensory canal (*ioc*, figs. 32—37, 41, 53, 55, 58, 68 A, 71 A, 72 A; pl. 3, fig. 3; pl. 8, fig. 1; pl. 9, figs. 1, 4; pls. 11—13; cf. pl. 2, fig. 1, *iocp*; pl. 6, fig. 3, ioc_c) of the Rhipidistid Crossopterygians is situated in the lachrymal. From this bone it continues forward through the lateral and medial rostrals, anastomosing with the corresponding canal of the opposite side in the tip of the snout.[1] During its passage through the anterior part of the lachrymal and through the lateral rostral the canal is situated far ventrally, along and about straight ventrally to the ventro-lateral margin of the ethmoidal region (figs. 53, 58, 72 A). Its ethmoidal commissure also lies far ventrally, more precisely ventrally to the tip of the ethmoidal region (*soc_c*, fig. 68 D).

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[1] The more recent restorations published of *Porolepis* (STENSIÖ 1932, fig. 30 B_1, B_2), *Holoptychius* (WESTOLL 1937), *Osteolepis* (GOODRICH 1919; WATSON 1926, fig. 3 A; SÄVE-SÖDERBERGH 1933 a, 1941) and other forms convey the impression that in Rhipidistid Crossopterygians there is an interruption of the infraorbital canal at the anterior end of the lachrymal. However, no such interruption exists.

The course of the infraorbital sensory canal in primitive *Coelacanthiformes* (figs. 32 A, 77; pl. 15, fig. 2; pl. 16, fig. 2; cf. figs. 73 B, 74 A; pl. 15, *gr_c ioc*) is fundamentally as in the Rhipidistid Crossopterygians. A particularly characteristic feature of the canal in *Coelacanthiformes* is that along the posterior part of the ethmoidal region it is situated considerably further dorsally than in the Rhipidistid Crossopterygians. Immediately in front of the orbital opening it turns upwards and passes along the lateral side of the postnasal wall (*w. pn*, fig. 73) after which it curves downwards and passes on forwards obliquely across the fenestra endonarina communis (*fe. en*). Together with the corresponding canal of the opposite side it forms an ethmoidal commissure which, as in the Rhipidistids, lies close ventrally to the anterior tip of the ethmoidal region.

The simple course of the sensory canals of the snout here described is found in primitive representatives of all three main groups. In the more specialized forms certain more complicated conditions may be encountered. These complications are caused above all by the development of anastomoses between the infraorbital and supraorbital canals.[1]

In *Eusthenopteron foordi* the supraorbital and infraorbital canals may at least sometimes be secondarily connected with one another between the fenestra endonarina anterior and the orbital opening. This connection consists of excessively branching tubes (cf. pl. 7) or of such tubes and a true canal (*comt*, pl. 7, fig. 2) passing down from the part of the supraorbital canal situated in the nasal series to the part of the infraorbital canal lying in the lachrymal. Between the nasal series of bones and the lachrymal it pierces the supraorbito-tectal.[2]

In Postdevonian, or at any rate in Postpalaeozoic Coelacanthids, for instance the undetermined Triassic form from East Greenland preliminarily described by NIELSEN (1936) and the recent *Latimeria* (J. L. B. SMITH 1939), the sensory canal system of the snout is fairly complicated. Owing to this and for other reasons an interpretation of the canals in the snout of Postdevonian Coelacanthids is very difficult. It is no wonder, therefore, that, as far as I can see, both NIELSEN and SMITH are to some extent seriously mistaken in their identifications of the sensory canals of the snout in the forms described by them. On the basis of the course of the sensory canals in Devonian Coelacanthids I shall here with the aid of my own observations on the Triassic form described by Nielsen and guided by the description and figures published by Smith on *Latimeria*, make an attempt to arrive at what I consider a more correct and satisfactory interpretation of the sensory canal system of the snout in Postdevonian Coelacanthids.

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[1] Certain of these anastomoses in Coelacanthids are possibly old formations (cf. pp. 602, 618).

[2] The presence of this connection was detected by the writer on an earlier occasion (JARVIK 1937, p. 77). Its existence has later been questioned by WESTOLL (1937 c, p. 519).

In the two Devonian forms *Nesides* and *Diplocercides* we find in the lateral rostral a fairly wide foramen (*f. com. trp*, fig. 77 A; pl. 16, fig. 2; see p. 569 below) through which the infraorbital sensory canal opens in a dorsal direction. This foramen which was overlooked by Stensiö (1937 a) lies at the corresponding place at which in the Postdevonian forms dealt with below (the Triassic form preliminary described by Nielsen, *Latimeria*) the lateral rostral is pierced by a commissure, the posterior transverse commissure (*com. trp*, fig. 32 B, C), between the infraorbital and supraorbital canals (see pp. 338, 584, 588). Judging from its position, the foramen must thus have given passage either to a corresponding commissure or to a large tube representing this commissure in an initial stage of development. Due to the fact that in the specimens available of both *Nesides* and *Diplocercides* the dermal bones of the posterior parts of the ethmoidal region are deficient and that the supraorbital sensory canal is known by its pores only (Stensiö 1937 a, fig. 2; pls. 2, 9; pl. 10, figs. 2, 3), it cannot for the present be decided which of the said two alternatives is true. In the two other Devonian forms so far known, *Euporosteus* (pl. 14; pl. 15, fig. 2; Stensiö 1937 a, figs. 9, 10) and *Dictyonosteus* (cf. p. 579 below), in which the supraorbital sensory canal is preserved, there is, as far as I can see, no lateral branch which might be considered to represent a dorsal part of a posterior transverse commissure, and in these two forms there was, therefore, at least no complete posterior transverse commissure. It is thus conceivable that also in *Nesides* and *Diplocercides* this commissure was not developed as such. The foramen *f. com. trp* in them through which the infraorbital sensory canal opens dorsally in the lateral rostral must therefore, at least for the present, be assumed to have transmitted only a strong dorsal tube (*com. trp*, fig. 32 A), a dorsal tube which is to be regarded as an initial stage towards the formation of the posterior transverse commissure of later Coelacanthids. As in *Euporosteus* and *Dictyonosteus* there is nothing preserved of the lateral rostral, it is impossible to make sure whether a corresponding dorsal tube was developed in them.

In the Triassic Coelacanthid form from East Greenland preliminarily described by Nielsen the sensory canal system of the snout is as follows (cf. pp. 583—585 below). The infraorbital sensory canal (*ioc*, fig. 32 B; *ioc. R. l*, *ioc. R. m*, fig. 80) pierces the lateral rostral in a longitudinal direction in a similar way as in the Devonian forms, after which it continues forwards through a single row of medial rostrals to anastomose with the corresponding canal of the other side. The foremost part of the canal that is situated in the anterior part of the lateral rostral and in the medial rostrals was overlooked by Nielsen. As far as it could be traced forwards, the supraorbital sensory canal (*soc*) runs mainly as in the Devonian forms. About opposite the anterior external nostril (*na*), where even in the Devonian forms (fig. 32 A) it lies close to the median line of the skull-roof, the canal is, however, here fused with the canal of the other side (fig. 32 B). Whether it continues further forwards and anastomoses anteriorly with the infraorbital canal at the corresponding place as in the Devonian forms could not be established with certainty (the most anterior part of

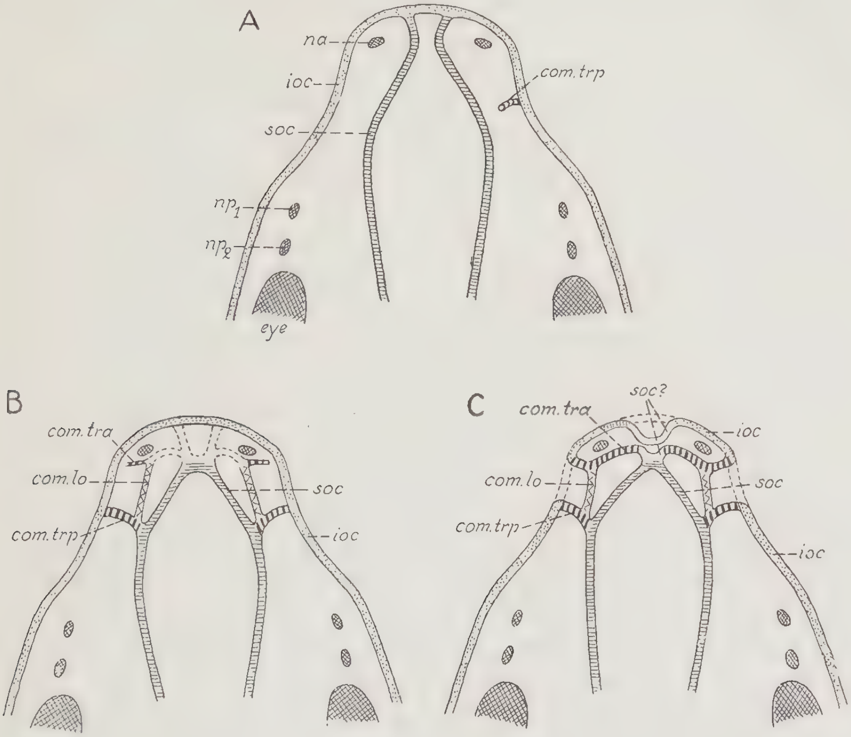

Fig. 32. Diagrams showing the sensory canals of the snout in *Coelacanthiformes*. Dorsal view. *A*, Devonian Coelacanthid. The left side of the figure shows the presumed primitive course of the canals, the right side shows in addition the posterior transverse commissural canal in an initial stage of development (*Nesides*, *Diplocercides*). *B*, the undetermined Triassic Coelacanthid from East Greenland, preliminarily described by Nielsen (1936). *C*, *Latimeria chalumnae* Smith.

com. lo, longitudinal commissural canal; *com. tra*, *com. trp*, anterior and posterior transverse commissural canals; *ioc*, infraorbital sensory canal; *na*, anterior external nostril; np_1, np_2, posterior external nostrils; *soc*, supraorbital sensory canal; *soc?*, canal probably representing anterior parts of supraorbital sensory canal.

the canal has therefore been denoted with broken lines in the restoration given in fig. 32 B). As noticed by NIELSEN, the supraorbital and infraorbital canals are connected with one another opposite the middle part of the lateral rostral. The two canals are actually in communication at this place by a short transverse commissural canal (*com. trp*, fig. 32 B) regarded by NIELSEN as the foremost part of the supraorbital canal. This commissural canal, situated at the corresponding place as the dorsal tube of the infraorbital canal in the Devonian forms *Nesides* and *Diplocercides*, constitutes the posterior transverse commissure between the supraorbital and infraorbital canals already referred to above. From the dorso-medial part of this commissure there issues a canal in a forward direction along the dorsal margin of the middle part of the lateral rostral. This canal, interpreted by NIELSEN as a part of the infraorbital canal, has here been termed the longitudinal commissure (*com. lo*, fig. 32 B). Anteriorly the longitudinal commissure as thus defined sends out a long tube in a ventro-lateral direction, a tube already observed by NIELSEN (1936, *v. b*, figs. 9, 14) and mentioned by him as a "ventrally directed small branch from the ethmoidal commissure of the infraorbital canals". This tube (*com. tra*, figs. 32 B, 80) passes downwards immediately behind the fenestra exonarina anterior (*fe. exa*, fig. 80; cf. fig. 32, *na*), but does not come down to the infraorbital canal. Though not yet connected with the infraorbital canal, this tube must obviously represent the anterior transverse commissure in *Latimeria* (fig. 32 C). Whether it continues medially to the anterior end of the longitudinal commissure so as to anastomose with the supraorbital canal could not be ascertained.

In the single specimen thus far caught of the recent form *Latimeria* SMITH (J. L. B. SMITH 1939) was unable with certainty to trace all the sensory canals of the snout. As far as our present knowledge goes, the sensory canals in *Latimeria* (figs. 32 C, 35) seem to be fundamentally as in the Triassic form from East Greenland, with the main difference, however, that the commissural sensory canals are somewhat more developed. The posterior transverse commissure (*com. trp*), comprising what SMITH regards as part of the supraorbital canal — by him termed the parafrontal canal (*a*) —, is well developed. From this canal issues, as in the Triassic form, a canal which passes forward and is situated along the dorsal margin of the middle part of the lateral rostral (bone No. 18 of SMITH's description). This canal, considered by SMITH to be part of the supraorbital canal, is the longitudinal commissure (*com. lo*). The longitudinal commissure is connected anteriorly with a transverse canal (*com. tra*, figs. 32 C, 35) which close behind the anterior external nostril forms a commissure between the supraorbital and infraorbital canals.

The latter transverse commissure, which includes both the canal lettered *h* by Smith and the foremost part of the "parafrontal canal" (*a*) of Smith's description that passes "to the lowest anterior point of 18" (J. L. B. Smith 1939, p. 49), is the anterior transverse commissure. The supraorbital canal (*soc*) is represented by the parafrontal canal (*a*) of Smith's terminology as far forwards as to the place where the bones 3, 5, and 6 meet (fig. 35), but besides that it includes also the canal *r* of Smith's description. Between the bones denoted by Smith by 8 and 8′ the supraorbital canal anastomoses in the median line with the corresponding canal of the opposite side. It is uncertain whether it continues forwards beyond this place, but it is not impossible that the most medial part of the canal *h* in Smith's terminology and one half of the median backward-curving part of the canal *g* of Smith's description may also belong to it (*soc*?, fig. 32 C). The infraorbital canal (*ioc*) comprises the following canals of Smith's description: 1) the infraorbital canal (*b*); 2) the canal situated in the posterior tube-shaped part of the lateral rostral, erroneously interpreted by Smith (1939, p. 49) as part of the supraorbital canal (*a*); and finally, 3) at least the main lateral part of the canal *g*. Whether, as in the fossil forms, the infraorbital sensory canal pierces also the anterior part of the lateral rostral situated in front of the posterior transverse commissure is not clear from the account given by Smith, but this is very likely the case. However, it is not quite inconceivable that this part of the infraorbital canal (denoted with broken lines in fig. 32 C) might have been reduced in connection with the complete development of the secondary commissures. Whether the original ethmoidal commissure between the infraorbital canals actually persists is uncertain. If represented by the backward-curving median part of the canal *g* of Smith's description, it must be assumed to have shifted secondarily backwards from its primary position on the very tip of the snout. As has already been intimated above, the said median part of the canal *g* may instead represent those foremost parts of the supraorbital canals of both sides that in the Devonian forms anastomose with the infraorbital canals. If this is so, the true ethmoidal commissure (in fig. 32 C denoted with broken lines) must either be secondarily absent or must have been overlooked by Smith.

The supraorbital sensory canal in the Coelacanthids, *Dictyonosteus* excepted (see p. 580 below), is wider than in other Crossopterygians and is throughout its extent situated between a medial and a lateral row of dermal bones (Stensiö 1921, p. 128, figs. 25, 43; 1932, p. 57, figs. 18, 19; 1937 a; Moy-Thomas 1935 a; 1937; Nielsen 1936; J. L. B. Smith 1939). The position of the canal between two rows of dermal bones was regarded by Nielsen (1936) as a primitive condition, an opinion which caused him to suggest a new theory for the interpretation of the dermal bones developed in relation to the canal in question, a new theory which on insufficient grounds was accepted by Stensiö (Stensiö 1937 a, pp. 28—30; cf. Pehrson 1940, pp. 23—26). As will be demonstrated below, the dermal bones forming the anterior parts of the skull-roof in fact show a striking agreement in their development and disposition in Coelacanthids and Rhipidistids. If these bones are interpreted according to Nielsen's theory, this leads, however, to impossible results. Certain of the bones which in the two groups agree well in shape, position, and other respects would then have to be considered of different origin. The supraorbitals in Coelacanthids (*So*, fig. 35; bones 11—16 in Smith's terminology) are according to Nielsen's theory fronto-supraorbitals (Säve-Söderbergh 1937 a, p. 261; Stensiö 1937 a, p. 30) and would therefore not be strictly homologous to the supraorbitals in the Rhipidistids (So, So_1, So_2, figs. 33, 34), which, being devoid of frontal components, are true supraorbitals. In reality Nielsen's theory renders a comparison of the dermal skeletons in Coelacanthids and other Crossopterygians quite difficult. One is therefore inclined to suspect that this theory must be dropped and that accordingly the position of the supraorbital canal between the longitudinal series of bones cannot be primitive. I shall now try to give a more natural and satisfactory explanation of the peculiar position of the supraorbital canal in Coelacanthids.

As is well known, the supraorbital canal in Coelacanthids is situated mainly in a deep groove in the lateral margin of the row of bones, the fronto-nasal series (Fr—Na_6—Na_1, fig. 35), that is situated medially to the canal (Nielsen 1936, pp. 22, 24; Stensiö 1937 a, p. 18; fig. 5; J. L. B. Smith 1939, p. 48). The remaining lateral part of the canal is housed in a fairly shallow groove in the medial margin of the row of bones on the lateral side of the canal, the supraorbito-tectal series of bones (*So*—*Te.p*—*Te.a*, fig. 35). This series of bones is also pierced by the very wide tubes of the canal, all of which are directed more or less strongly laterally. As the tubes widen in a basal direction towards the canal, it is not inconceivable that the lateral part of the canal situated in the supraorbito-tectal series of bones may have arisen by a confluence and fusion of the most proximal parts of the tubes. On the other hand, in Rhipidistid Crossopterygians, e. g. *Eusthenopteron* (fig. 34; pl. 8, fig. 2; Jarvik 1937, fig. 6) and *Osteolepis* (Säve-Söderbergh 1933 a, figs. 6, 19; 1941, fig. 3 B), the supraorbital canal is relatively much narrower than in Coelacanthids and lies entirely enclosed in the frontal and nasals. However, it runs in them in the lateral part of the frontal and, as in the Coelacanthids, it gives off tubes directed laterally, which in *Eusthenopteron* penetrate into the supraorbitals. It is easily seen that if excessively developed in the same manner as in the Coelacanthids, e. g. *Euporosteus* (pl. 14) and *Latimeria* (fig. 35), the supraorbital canal in Rhipidistids would run in or at any event close to the suture between the frontal and the supraorbitals. In *Dictyonosteus* which presumably is the oldest known Coelacanthid (cf. pp. 579—580 below), the supraorbital canal is relatively not wider than in the Rhipidistids and as in these it is enclosed in the lateral part of the frontal (Stensiö 1921, fig. 58; 1922 a, fig. 3) and pierces at least the foremost element of the nasal series (see p. 580). In the non-Crossopterygian fishes (see for instance Holmgren and Stensiö 1936) the supraorbital canal is normally narrow[1] and as far as we know it never runs between a medial and a lateral series of bones (as regards Acanthodians see p. 342 below). What has now been said tends to show, as far as I can see, that the sutural course of the supraorbital canal in typical Coelacanthids is secondary and due simply to the excessive development of the canal. This opinion has previously been advanced by Säve-Söderbergh (1933 a, p. 111).

The embryological researches by Pehrson (1922), according to which in *Amia* inter alia the dermal bones pierced by the supraorbital canal are of a paired origin, are considered by Nielsen (1936, p. 26) to support his theory.

In his studies of *Amia* Pehrson (1922; 1940) has found that certain of the sensory canal bones, more precisely the nasal and frontal, both pierced by the supraorbital canal, the supratemporo-intertemporal, pierced by the otic part of the infraorbital canal and the postotic canal, the preopercular and the splenial components of the complex dentalo-splenial and angular-splenial developed in relation to the preoperculo-mandibular canal, "are derived from binary primordia, as a rule developing one on each side of a neuromast" (Pehrson 1940, p. 23). Pehrson attaches much importance to this condition which indicates, in his opinion, that the sensory canals mentioned in the primitive ancestors of *Amia* must have passed between two rows of sensory canal bones. The interpretation of the binary primordia and the homologisation of dermal bones based on this interpretation of the primordia that were given by Pehrson in his earlier work (1922) have been criticized by Säve-Söderbergh (1933 a) and Hammarberg (1937). According to Hammarberg, who has studied the embryonic development of the dermal bones in *Lepidosteus*, only the posterior parts of the nasal arise in this form from binary primordia, whereas the anterior part of the nasal and all other sensory canal bones are derived from single primordia. HAMMARBERG (1937, p. 275) is of the opinion, however, that there are no true binary primordia. The primordia considered to be binary are only apparently so, being secondarily more or less clearly subdivided for instance by the sensory nerves each of which in order to reach its sense organ (neuromast) traverses the underlying primordium through a wide opening (cf. AUMONIER 1941, p. 20). If HAMMARBERG is right in this, and there is in my opinion no doubt but that he is, it follows of course that the presence of "binary primordia" in *Amia* and *Lepidosteus* cannot be a primitive character due to a primary relation between the sensory canals and the dermal bones. An additional support for HAMMARBERG's opinion on this point is supplied by the fact that in *Palaeonisciformes*, which probably include the primitive ancestors of *Amia* and *Lepidosteus*, the sensory canals have never been found to have a sutural course.

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[1] In certain of these forms, as the recent Macrurids (Pfüller 1914), the sensory canals may sometimes be much widened secondarily.

In Coelacanthids and in Acanthodians PEHRSON (1940, pp. 22—26) believes that he can find a parallel to the "binary primordia" in the larval *Amia*. That this is probably not so in the Coelacanthids is clear from what has already been said above. Concerning the Acanthodians PEHRSON (p. 22) states that according to WATSON (1937) . . . "the sensory lateral line always runs between each two of the dermal bones" . . . It is evident, however, that PEHRSON has not paid enough attention to WATSON's descriptions, for what WATSON actually says of the sensory canals in the head of *Diplacanthus striatus* is as follows. "As in many other Acanthodians the anterior part of the system is peculiar in that the actual canal runs through a chain of short bony cylinders. These may be, and probably are, independent of the normal bones. Usually the canal surrounded by the apparently single cylinder lies between two rows of dermal bones. Posteriorly these cylinders are absent and the course of the canal can only be determined from the two rows of scales, a matter of difficulty especially on the body" (WATSON 1937, pp. 92—93). The bony cylinders in *Diplacanthus* are highly suggestive of the cylindrical ossicles that form the sensory canal bones in embryonic stages of several fishes (see HAMMARBERG 1937, pp. 309—315) and they must certainly be regarded as true sensory canal bones. What WATSON means by "the anterior part of the system" in the above quotation is not easily understood, but from his descriptions otherwise and from his figures (WATSON 1937, pp. 67—75; figs. 5, 9) it seems to be clear that besides the canals on the anterior parts of the head also the otic part of the infraorbital canal, the postotic canal, and the "hyomandibular" canal (preopercular canal?) are associated with a single chain of bones only. All of the canals which in *Amia* are connected with "binary primordia" seem thus in Acanthodians to pass in a single row of special sensory canal bones.

The conditions in Acanthodians thus do not support PEHRSON's opinion. As in all fossil fishes the sensory canals are either enclosed in dermal bones or pass in grooves on the outside of dermal bones, it is quite evident that no support whatsoever is to be found in lower fossil vertebrates for PEHRSON's opinion concerning the phyletic importance of the "binary primordia" in *Amia.*

As may be gathered from the above account, I am unable to accept NIELSEN's theory for the interpretation of those of the dermal bones in Crossopterygians, Dipnoans, and Actinopterygians that are developed in relation to the supraorbital sensory canal. As far as I can see, this theory must be dropped. Nor can I accept the homologizations of dermal bones made by PEHRSON on the basis of the "binary primordia" in *Amia.* These homologizations do not seem to be maintainable any longer.

For the purpose of illustrating the general disposition of the dermal bones in the snout of Crossopterygians, a type for each of the three main groups of Crossopterygians will here be described. The types chosen are: *Holoptychius* sp. from East Greenland for the *Porolepiformes*, *Eusthenopteron foordi* for the *Osteolepiformes*, and the recent *Latimeria chalumnae* for the *Coelacanthiformes.*

The terminology here applied to the bones of the fronto-ethmoidal shield is the one currently used by Swedish writers (STENSIÖ 1921, p. 144; SÄVE-SÖDERBERGH 1932 a, pp. 7—10; 1933 a, pp. 9—10; 1935, pp. 7—10; HOLMGREN and STENSIÖ 1936, pp. 355—356) though with certain corrections. It should be pointed out that I do not intend to take up a position with reference to the difficult question of the homologization of the dermal bones of the Crossopterygians with those of other groups. Occasionally certain comments must, however, be made on the general homologies of some of the bones.

WESTOLL has recently maintained (WESTOLL 1936, p. 166; 1938; 1938 a; 1940, pp. 71—72; cf. ROMER 1937, p. 52; 1941, pp. 156—159) that the frontal in Crossopterygians is the homologue of the parietal in Tetrapods. A closer comparison of the frontal in *Eusthenopteron* (*Fr*, figs. 34, 50, 55, 65 A, 68 A; pl. 7) with the frontal in Anuran tadpoles (see for instance W. K. PARKER 1871, pl. 7, figs. 3, 5; pl. 8, figs. 1, 7) and the frontal component of the compound fronto-parietal[1] in adult

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[1] In his studies of young and transforming larvae of various *Anura,* EATON (1939) was unable to find the parietal and the frontal as independent elements. He therefore drew the conclusion that the fronto-parietal in Anurans probably cannot be a compound bone. Of previous papers on this subject he refers only to W. K. PARKER's description of the development of the skull in the common frog (1871), expressing the opinion that PARKER's observations are wrong. It is noticeable, however, that the

Anurans (*Fr-Pa*, figs. 23 A, 24, 66, 69; see also Gaupp 1905, fig. 377; Reinbach 1939, fig. 10; pls. 13, 14) shows, however, that these two bones agree in so many important characters that it can hardly be doubted that they are homologous formations. Quite as the frontal components of the Anuran fronto-parietals, the frontals in *Eusthenopteron* cover the dorsal side of the orbitotemporal region of the endocranium and in the suture between them lies the pineal foramen both in *Eusthenopteron* and in Anurans (Winterhalter 1931; Paterson 1939, p. 184; pl. 15, fig. 26). In its earliest stages of development so far observed the frontal in Anuran tadpoles consists of "eine zarte, kleine, in die Richtung von vorne nach hinten gestellte Knochennadel medial von der mittleren Augengegend" (Erdmann 1933, p. 605). This "Knochennadel" lies about opposite the posterior end of the hemisphere of its side of the forebrain (Eaton 1939, fig. 1 A). In *Eusthenopteron* the centre of radiation of the frontal lies underneath the point where the anterior pit-line (*apl*, fig. 34) crosses the supraorbital sensory canal (*soc*) and is thus also situated "medial von der mittleren Augengegend" and about opposite the posterior end of the hemispheral portion of the cranial cavity (*p. hem*, fig. 57 A—C). Judging from the position of its centre of radiation, the frontal in *Eusthenopteron* must have arisen embryologically exactly at the corresponding spot in the skull as the frontal in *Anura*. It is thus evident that Westoll's general statement that the Crossopterygian frontal is the homologue of the Tetrapod parietal cannot possibly be true as regards the Osteolepiform Crossopterygians and *Anura*. It may be added that the frontal in Osteolepiform Crossopterygians and Anurans in all probability is homologous also to the very similarly situated frontal in mammals (see e. g. De Beer 1937; pl. 112, figs. 2, 3; Stadtmüller 1936 a; figs. 640, 659). On the other hand, as will be shown in a future work, it is very likely that the frontal in *Eusthenopteron* and Osteolepiform Crossopterygians in general is homologous to the bone in Stegocephalians (and Urodeles?; cf. below p. 415) that is currently termed parietal. If my above opinions are true, it follows of course that the frontal of our current terminology is not homologous throughout the Tetrapods, and that the terms of the dermal bones in lower Tetrapods confirmed by the Nomenclature Committee of 1917 (Gregory 1917) will have to be revised.

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parietal and the frontal have been observed as independent elements by several writers not only in the tadpoles of the common frog (Dugès 1835, p. 18; pl. 13, fig. 70; Erdmann 1933, p. 605; cf. also De Beer 1937, p. 208; pl. 78, figs. 1, 3), but also in the tadpoles of *Bufo vulgaris, Xenopus (Dactylethra) capensis, Rana pipiens, Pseudis paradoxa* (W. K. Parker 1876; pl. 54, fig. 3; pl. 57, fig. 3; pl. 58, fig. 2; 1881; pl. 3, fig. 4; pl. 11, fig. 6; pl. 12, figs. 1, 2, 4), and *Pelobates fuscus* (Sewertzoff 1891). The current opinion that the Anuran fronto-parietal is a compound bone thus seems to be so well established that it can hardly be questioned.

The bone in *Eusthenopteron* that is termed the anterior tectal in this work (*Te. a*, fig. 34) has a position which renders it at any rate very likely that it is the homologue of the nasal in *Anura* (p. 549, fig. 68; cf. p. 415). The opinion generally accepted hitherto that the nasal in Tetrapods represents one or several of the nasal elements of the Crossopterygians (Gregory 1915, p. 335; Säve-Söderbergh 1932 a, pp. 87—92; 1935 pp. 118—119; Westoll 1938; 1940, p. 71; cf. also for instance Goodrich 1930; Romer 1933) cannot, therefore, be regarded as definitely settled.

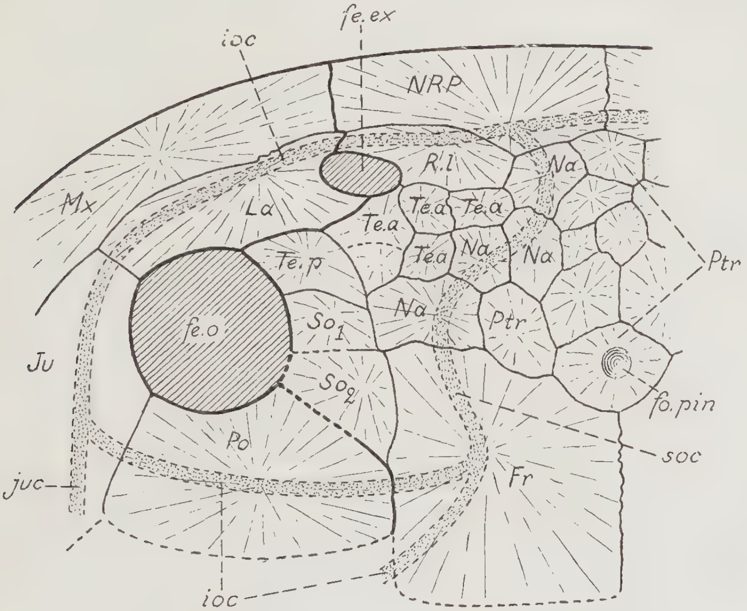

Fig. 33. *Holoptychius* sp. Sketch of the bones and sensory canals of the right half of the fronto-ethmoidal shield and of the anterior part of the right cheek. Ventral aspect. The dermal bones spread out into one plane. Restoration made after two specimens from the Upper Devonian of East Greenland, both of which belong to the Zoological Museum of the University of Copenhagen. 1 ¹/₄ approximately.

Fr, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *NRP*, naso-rostro-premaxillary; *Po*, postorbital; *Ptr*, postrostral; *R. l*, lateral rostral; So_1, So_2, supraorbital; *Te. a*, anterior tectal; *Te. p*, posterior tectal; *fe. ex*, fenestra exonarina communis; *fe. o*, orbital opening; *ioc*, infraorbital sensory canal; *juc*, jugal sensory canal; *soc*, supraorbital sensory canal; *fo. pin*, pit, probably for the pineal organ.

In fishes the sensory canals are, as we have long known, of great use for the interpretation and homologization of the dermal bones. When used for such a purpose, they must, however, first be clearly identified. If we want to compare one or several sensory canal bones in a certain form with one or more similarly situated bones in another form, we must first make sure whether the sensory canal or canals related to those bones are homologous in the two forms, which has not always been done. In *Palaeonisciformes* (fig. 85), *Saurichthys* (Stensiö 1925), sturgeons (Allis 1904), and other lower Actinopterygians, the sensory canal, which is held to be the foremost part of the supraorbital canal, curves laterally and downwards above the anterior parts of the orbital opening and runs down between the anterior and posterior external nostrils. In *Palaeonisciformes* (Moy-Thomas 1939 a, pp. 110—111) and *Saurichthys* (Stensiö 1925, p. 114; fig. 21) it anastomoses with the infraorbital canal far behind the tip of the snout. Though at least in sturgeons (Allis 1904; Norris 1925) it is supplied by the r. ophthalmicus lateralis, this canal can hardly be homologous to the anterior part of the supraorbital canal in Crossopterygians, which, as we have seen, has quite a different position and quite different relations to the external nostrils (figs. 32—35). Under these conditions it may be questioned whether the bone or bones in the lower Actinopterygians that are pierced by the foremost part of the "supraorbital canal" and which are usually known as nasal or nasals are to be regarded as true homologues of the nasals in Crossopterygians (cf. pp. 615—619).

We shall now proceed to a brief account of the general disposition of the dermal bones of the snout in Crossopterygians.

The part of the infraorbital sensory canal that is situated along the ethmoidal region pierces a paired row of bones, the rostrals, in all three main Crossopterygian groups (figs. 33—35, 52 B, 53, 58, 68 A, 70 A, 71 A, 77, 80, 81, 83 B, 86 A; pl. 3, fig. 3; pl. 6, figs. 2, 3; pl. 7; pl. 8, fig. 3; pl. 9, figs. 1, 4; pls. 10—12; pl. 15, fig. 2; pl. 16, fig. 2). In all the groups we find a large lateral rostral (*R. l*; pp. 449—450, 567—571)[1] and one (*Eustheno-*

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[1] That the lateral rostral in *Eusthenopteron* is pierced by the infraorbital canal was pointed out already in a previous paper (Jarvik 1937, p. 119). Later on it has, however, been stated by Westoll (1937 c, pp. 518—519; 1940, p. 72) that this is not true, but that the lateral rostral possibly may enclose the infraorbital canal fortuitously and secondarily. Westoll says concerning this condition in *Eusthenopteron traquairi* (Westoll 1937 c, p. 514) that during its course laterally from the very tip of the snout "the ethmoid commissure runs laterally as though to enter the suture between the 'premaxillary' and the 'lateral rostral', and then turns ventrally and ends blindly". Not only in *Eusthenopteron foordi* (figs. 53, 58, 86 A; pl. 6, fig. 2; pl. 9, figs. 1, 4), but also in *Porolepis* (pl. 3, fig. 3) and *Holoptychius* (fig. 33), however, the lateral rostral is clearly pierced by the infraorbital canal. In the two last-mentioned forms the canal passes through the centre of radiation of the bone. Whether this is the case also in *Eusthenopteron* could not be definitely decided, but this much is obvious, however, that if the canal in this form does not pierce the very centre of radiation it passes very close to it. In the Coelacanthids the lateral rostral (figs. 77, 80, 83 B; pl. 16, fig. 2) has the shape of a tube, which surrounds the infraorbital canal and in these forms also the lateral rostral is thus pierced by the infraorbital canal. Under these circumstances it is obvious that the bone in question must be constantly developed in relation to the infraorbital canal; from which follows that its relation to this sensory canal must be primary and not fortuitous and secondary. The term lateral rostral must therefore be retained for it, whereas the new

pteron) or several (*Latimeria*) medial rostrals (*R. m*; cf. p. 602). Behind the lateral rostral lies the lachrymal (*La*; pp. 407—408, 414, 548) which in Coelacanthids is fused with the jugal to a compound lachrymo-jugal (*La-Ju*, fig. 77 A, B). The lachrymal in *Eusthenopteron* and *Holoptychius* belongs to the palatoquadrate-cheek complex, but it extends so far forwards that its anterior portion is situated laterally to the postero-ventral part of the ethmoidal region. However, it has no contact with the actual ethmoidal region, but is separated from it by the postero-ventral part of the lateral rostral, which it overlaps. The anterior portion of the lachrymo-jugal of Coelacanthids also goes forwards into the snout and is situated laterally to the posterior part of the ethmoidal region. It does not overlap the lateral rostral, but lies entirely behind it and rests directly against the ethmoidal region (cf. figs. 73 B, 74, 75, 76 B, *ar. La-Ju*). Ventrally to the rostrals there is a paired tooth-bearing premaxillary (*Pmx*) the antero-medial half of which in *Eusthenopteron* and *Holoptychius* is as a rule fused with the overlapping medial rostral so as to form a compound bone, the rostro-premaxillary.[1] In the majority of the specimens of *Eusthenopteron* available, however, also the foremost nasal (nasal 1) is fused with the rostro-premaxillary. The "premaxillary" in *Eusthenopteron* is therefore in most cases a naso-rostro-premaxillary formed by the fusion of a premaxillary proper, a medial rostral, and the foremost nasal (*NRP*, NRP_1, NRP_2, NRP_3, figs. 34, 56, 60, 68 A, 72 A, 87 A; pl. 6, figs. 1, 2; pl. 8, fig. 1; pl. 9, figs. 1, 3; pl. 10; pl. 11, figs. 1, 2, 4).[2] Also in *Holoptychius* there seems to be a naso-rostro-premaxillary (*NRP*, fig. 33) or at

term prenarial suggested by WESTOLL must be rejected. The term prenarial is also inappropriate for other reasons. Firstly, as has already been pointed out (JARVIK 1937, p. 123; cf. p. 535 below), the bone is the true homologue of the septomaxillary or narial (cf. foot-note on p. 249) in *Anura* and secondly it often lies postero-ventrally and not anteriorly to the anterior external nostril (see figs. 34, 68 A). As in the various Crossopterygians examined by me the infraorbital canal thus constantly pierces the lateral rostral thence to continue backwards through the lachrymal or the lachrymo-jugal (in the Coelacanthids), it is extremely likely that this is normally the case also in *Eusthenopteron traquairi*.

[1] In one specimen of *Eusthenopteron* the premaxillary has been found as a completely independent bone, separated from the medial rostral by a distinct suture (pl. 8, figs. 1, 3; pl. 9, fig. 2). In those specimens in which there is no suture between the premaxillary and medial rostral it is difficult to make out whether we are concerned with a true fusion or with a simple growing together of the two bones. That this cannot be decided with full certainty is due to the fact that the premaxillary to a large extent consists of bases of teeth which makes its radiating structure very obscure.

[2] Since the premaxillary has in one case been found as an independent bone in *Eusthenopteron* and since in addition it is independent in Coelacanthids it follows of course that WESTOLL's interpretation of the compound rostro-premaxillary or naso-rostro-premaxillary of the Rhipidistid Crossopterygians as a "dentigerous rostral" (WESTOLL 1936, p. 165; 1937 c, p. 509; 1940, p. 71) cannot possibly be true.

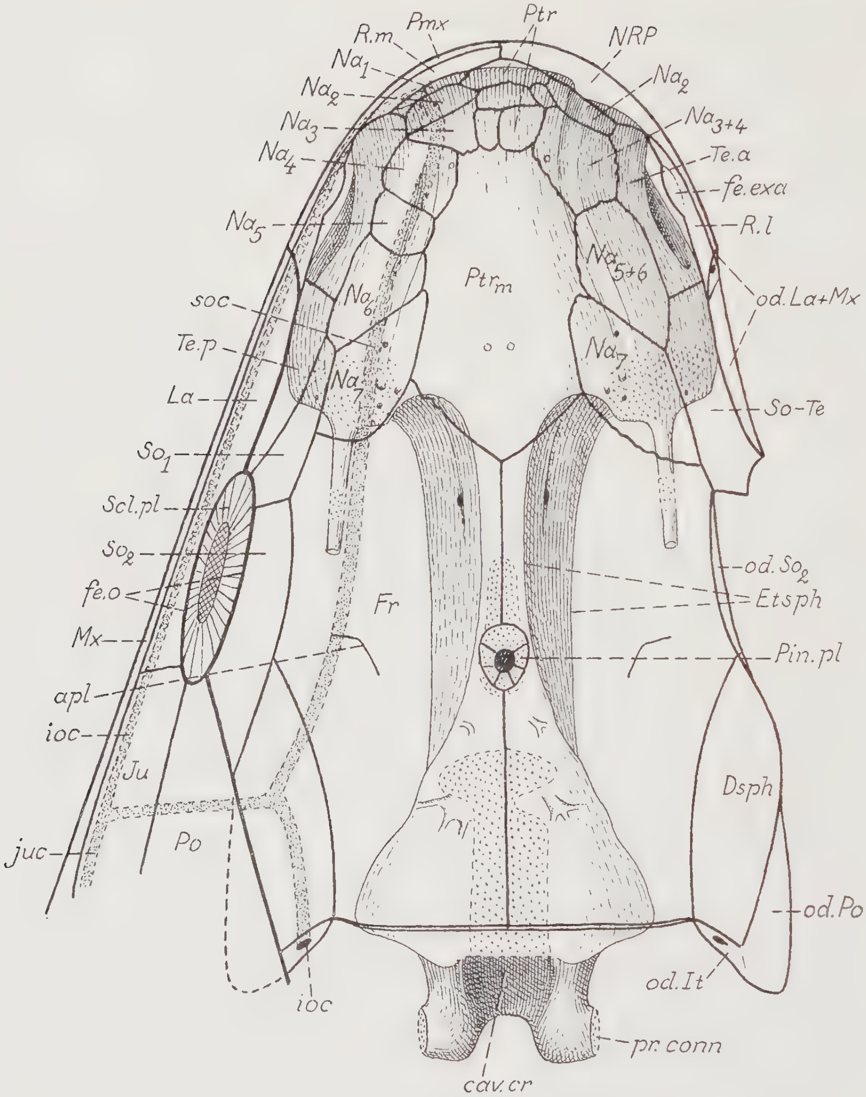
R.m
Pmx
Ptr
NRP
Na1
Na2
Na3
Na4
Na5
Na2
Na3+4
Te.a
fe.exa
R.l
Na5+6
Ptrm
Na6
od.La+Mx
soc
Te.p
La
Na7
Na7
So-Te
So1
Scl.pl
So2
fe.o
Mx
Fr
od.So2
Etsph
Pin.pl
apl
ioc
Ju
Dsph
juc
Po
od.Po
od.It
ioc
pr.conn
cav.cr

Fig. 34. *Eusthenopteron foordi* Whiteaves. Restoration showing the fronto-ethmoidal shield and the dermal bones of the anterior parts of the left cheek in their position in relation to each other, to the sensory canals, and to the ethmosphenoid. Dorsal aspect. On the left side all seven nasal elements, the medial rostral, the premaxillary, the posterior tectal, and the anterior supraorbital are shown as independent bone plates. On the right side the foremost nasal element forms part of the naso-rostro-premaxillary, whereas certain other nasal elements are fused with each other. The posterior supraorbital of the right side omitted. $^5/_2$.

Dsph, dermosphenotic; *Etsph,* ethmosphenoid; *Fr,* frontal; *Ju,* jugal; *La,* lachrymal; *Mx,* maxillary; *NRP,* naso-rostro-premaxillary, formed by fusion of the nasal 1, the medial rostral, and the premaxillary; Na_1—Na_7, nasals 1—7; Na_{3+4}, compound nasal formed by fusion of nasals 3 and 4; Na_{5+6}, compound nasal formed by fusion of nasals 5 and 6; *Pin.pl,* pineal plates; *Pmx,* premaxillary; *Po,* postorbital; *Ptr,* postrostral;

any rate a rostro-premaxillary. In *Eusthenopteron* and presumably also in *Holoptychius* the premaxillary proper (the premaxillary component of the rostro-premaxillary or naso-rostro-premaxillary) lies entirely below the endocranium and is not in direct connection with it, being separated from it by the palatal processes of the medial and lateral rostrals (see figs. 53, 58). The premaxillary proper in *Latimeria* which is not fused with the above-lying bones, is apparently represented by a few small paired tooth-bearing plates described by J. L. B. SMITH (1939, p. 68; *90*, fig. 10) as rostral dental plates. On the other hand, the premaxillary proper in fossil Coelacanthids, which is also an independent bone, is better developed and is not subdivided into smaller elements (fig. 81; cf. NIELSEN 1936, figs. 14, 15). In the Rhipidistid Crossopterygians the maxillary (*Mx*, figs. 33, 34, 41, 55, 56, 68 A) lies along the oral border of the snout behind the premaxillary. It forms part of the palatoquadrate-cheek complex but its foremost part stretches forwards ventrolaterally to the ethmoidal region, though it is not in contact with that region. In Coelacanthids the maxillary seems to be entirely absent (cf. pp. 606—607 below).[1]

Around the anterior part of each supraorbital canal there are developed several nasals (*Na*, Na_1—Na_7) which together form the nasal series (figs. 33—35, 46 A, 50, 52 B, 53, 55, 58, 65 A, 68 A, 83 B; pl. 6, fig. 1; pl. 7; pl. 14, fig. 2; pl. 15, fig. 2). In *Eusthenopteron* there are at most 7 nasal elements (fig. 34, left side). Of these, the foremost, as we have seen, usually forms part of the naso-rostro-premaxillary, whereas the others either remain independent or fuse with each other in various ways. Due to such fusions there are generally only 3—4 independent nasals, most or all of which are compound. In *Holoptychius* the maximum number of independent nasal elements is 6. In addition, this form at least probably has a seventh, foremost nasal element, which is included in the compound "premaxillary" (naso-rostro-premaxillary?). Finally, in

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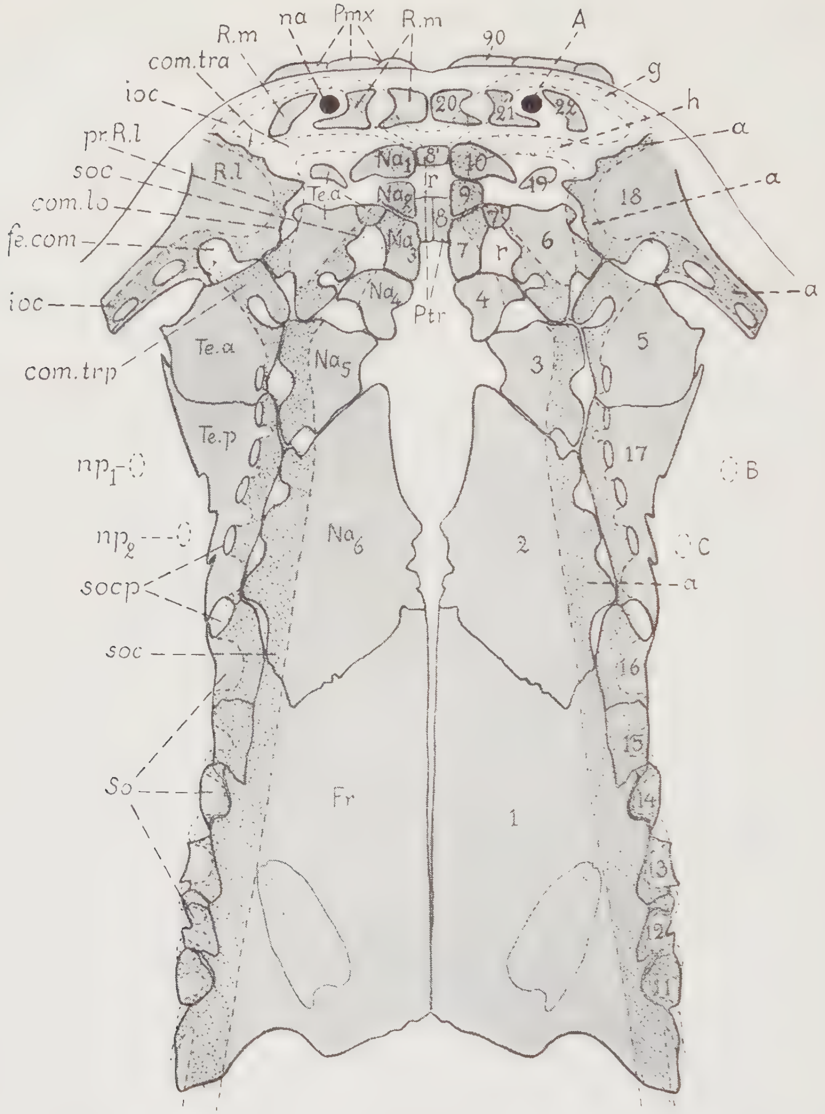
[1] The bone interpreted by NIELSEN (1936, p. 33; figs. 9, 10, 15) as a maxillary in the Triassic form from East Greenland preliminarily described by him is a tooth-bearing plate, which presumably belongs to the lower jaw. It seems to correspond to one of "the dental plates of the dentary" in *Latimeria* (J. L. B. SMITH 1939, p. 63; fig. 8, bone 44').

Ptr_m, posterior median postrostral; *R. l*, lateral rostral; *R. m*, medial rostral; *Scl. pl*, sclerotic plates; So_1, So_2, anterior and posterior supraorbital; *So-Te*, supraorbito-tectal, formed by fusion of anterior supraorbital and posterior tectal; *Te. a*, anterior tectal; *Te. p*, posterior tectal; *apl*, anterior pit-line of skull-roof; *cav. cr*, cranial cavity; *fe. exa*, fenestra exonarina anterior; *fe. o*, orbital opening; *ioc*, infraorbital sensory canal; *juc*, jugal sensory canal; *od. It*, area of dermosphenotic overlapped by intertemporal; *od. La* + *Mx*, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *od. Po*, area of dermosphenotic overlapped by postorbital; *od.* So_2, area of frontal and dermosphenotic overlapped by posterior supraorbital; *pr. conn*, processus connectens; *soc*, supraorbital sensory canal.


na
Pmx
R.m
R.m
A
90
com.tra
g
ioc
h
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pr.R.l
soc
R.l
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Te.a
Na1
8
10
ir
Na2
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19
18
fe.com
Na3
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7
r
6
ioc
Na4
Ptr
4
a
Te.a
Na5
3
5
com.trp
Te.p
17
np1
B
np2
Na6
2
C
socp
a
soc
16
15
So
Fr
1
14
13
12
11
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21
22

Fig. 35. *Latimeria chalumnae* Smith. Sketch showing the dermal bones and sensory canals of the fronto-ethmoidal shield. Compilation after J. L. B. Smith (1939, figs. 3 and 4). Smith's original lettering retained on the right half of the figure. $^3/_4$ approximately.

Fr, frontal; Na_1—Na_6, nasals 1—6; *Pmx*, premaxillary; *Ptr*, postrostral; *R. l*, lateral rostral; *R. m*, medial rostrals; *So*, supraorbital; *Te. a*, anterior tectals; *Te. p*, posterior tectal; *com. lo*, longitudinal commissural sensory canal; *com. tra*, *com. trp*, anterior and posterior transverse commissural sensory canals; *fe. com*, fenestra in dermal cranial roof, filled by posterior transverse commissural sensory canal; *ioc*, infraorbital sensory canal; *na*, anterior nostril; np_1, np_2, posterior nostrils; *pr. R. l*, antero-dorsal process of lateral rostral; *socp*, pores of supraorbital sensory canal.

Lettering used by Smith and interpretations given by him. *A*, rostral narial aperture; *B*, *C*, lower and upper lateral narial apertures; *a*, parafrontal canal; *g*, rostral com-

Latimeria, if the interpretation given in fig. 35 is correct, there are also six nasals. The hindmost and very large nasal in *Latimeria* is, however, probably a compound bone, formed by the fusion of two nasal elements. Judging from these conditions it is thus likely that the total number of nasal elements in *Eusthenopteron*, *Holoptychius*, and *Latimeria* is normally 7.

Posteriorly and postero-medially to the rostrals and laterally to the nasals we find a varying number of paired bones which have hitherto been very imperfectly known (*Te. a*, *Te. p*, figs. 33—35, 46 A, 52 B, 53, 58, 65 A, 68 A, 77 A, B, 83 B; pl. 6, figs. 1, 2; pl. 7; pl. 9, figs. 1, 4; pl. 10; pl. 11, fig. 4; pl. 14; pl. 15, fig. 2; pl. 16, fig. 4; pl. 17, fig. 2). For these bones, usually called antorbitals, I have here suggested the new term tectals (cf. p. 249 above). The reason why the previous term antorbitals has not been retained is that these bones cannot possibly be homologous to the antorbital in Actinopterygians (cf. Westoll 1937 c, p. 519) which is pierced by the infraorbital sensory canal and seems to be more comparable to the lateral rostral of the Crossopterygians (cf. p. 618). The tectals as here defined form together a longitudinal series of bones in the anterior prolongation of the series of supraorbitals (So, So_1, So_2). In *Eusthenopteron* there are only two, one anterior (pp. 448—449; cf. foot-note on p. 489) and one posterior, whereas in *Holoptychius* and *Latimeria* there are one posterior and several anterior tectals. The posterior tectal (*Te. p*) extends as far backwards as to form part of the anterior border of the orbital opening. In *Eusthenopteron* it is often fused with the anterior supraorbital to a compound supraorbito-tectal (*So-Te*).[1] In fossil Coelacanthids it is pierced by the bipartite fenestra exonarina posterior (fe_1exp, fe_2exp, fig. 77 A; pl. 16, fig. 4), whereas in *Latimeria*, owing to a reduction of its ventro-lateral part, it is situated dorsally to the said fenestra. The anterior tectal (*Eusthenopteron*) or one of the anterior tectals (*Holoptychius*) participates more or less in the dorsal boundary of the fenestra exonarina anterior.

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[1] The occurrence of a compound bone in *Eusthenopteron* formed by a fusion of the posterior tectal, then called antorbital, with the foremost supraorbital has been maintained by me on an earlier occasion (Jarvik 1937, p. 75; "supraorbito-antorbital"). The compound origin of this bone has been strongly questioned by Westoll (1937 c, p. 517). Since it is now clear that the posterior tectal and the anterior supraorbital are independent in certain specimens of *Eusthenopteron* and since, as far as we know, these two bones are normally independent both in *Porolepiformes* and *Coelacanthiformes*, Westoll's objection is groundless.

missural canal; *h*, posterior rostral commissural canal; *r*, fronto-rostral commissural canal; *1*, frontal; *2*, frontal; *3*, fronto-nasal; *4*, postrostral; *5*, naso-antorbital; *6*, rostro-nasal; *7*, *7′*, rostral; *8*, meso-rostral; *8′*, inter-rostral; *9*, *10*, rostral; *11*, *12*, *13*, *14*, *15*, *16*, parafrontal; *17*, parafronto-antorbital; *18*, latero-rostro-nasal; *19*, rostral; *20*, inner-rostral; *21*, mid-rostral; *22*, outer-rostral; *90*, rostral dental plates.

Between the nasal series of both sides are situated the postrostrals which may be paired or unpaired or both (*Ptr*, Ptr_m, Ptr_a, figs. 33—35, 46 A, 50, 53, 55, 58, 65 A; 68 A; pl. 6, fig. 1; pl. 7, fig. 2; pl. 11, figs. 3—5; pl. 12, fig. 5; pl. 14, fig. 1). These bones vary considerably in number (cf. Westoll 1936). In *Eusthenopteron* there is normally one large unpaired posterior median postrostral (Ptr_m) and several small anterior postrostrals (*Ptr*). In *Holoptychius* the postrostrals (*Ptr*) are numerous, but all of them are fairly small. The hindmost one in *Holoptychius*, which is a median unpaired plate, exhibits a pit (*fo. pin*, fig. 33) on its lower side, a pit which probably housed the pineal organ. In the *Coelacanthiformes* the postrostral series is more weakly developed than in the other two main groups of Crossopterygians, and in *Latimeria* it is represented only by one anterior unpaired and one small posterior paired element.[1]

Immediately behind the nasal and postrostral series follows the paired frontal (*Fr*) which is always a large bone (figs. 33—35, 50, 55, 65 A, 68 A; pl. 7; cf. pp. 343—344). In *Eusthenopteron* (figs. 34, 65 A, 68 A) this bone reaches so far forwards that its foremost part, overlapped by the hindmost nasal and posterior median postrostral, covers the hindmost part of the dorsal face of the ethmoidal region. In *Holoptychius* it has a less forward extent, but its relations to the endocranium are not known in this form. Also in *Latimeria* its forward extent is smaller than in *Eusthenopteron*.

The premaxillaries, rostrals, postrostrals, nasals, tectals, and, at least in certain forms the foremost part of the frontals form together the ethmoidal shield, which covers the whole curved upper side of the ethmoidal region. In *Porolepiformes* and *Osteolepiformes* the postero-ventro-lateral corner of the ethmoidal shield is to a considerable extent (*od. La*+*Mx*, *od. La*, figs. 34, 40 B, 50, 52 B, 62 A, 63, 68 A) overlapped by the lachrymal and the maxillary, which, as has been pointed out, both belong to the palatoquadrate-cheek complex.

The lower (oral) side of the ethmoidal region is covered by the paired vomer (*Vo*, Vo_d, *la. Vo*, *pr. Vo*, $pr_m Vo$, $pr_p Vo$, figs. 37 A, 44, 46 A, 50, 52 B, 53, 55, 56, 58, 60, 62 A, 64 A, 65 A, 81, 87 A; pl. 5, fig. 2; pl. 6, fig. 1; pl. 8; pl. 9, figs. 2—4; pl. 11, figs. 2—6; pls. 12, 13), by Smith (J. L. B. Smith 1939, p. 69; *91*, fig. 10) erroneously termed postrostral plate in *Latimeria* (cf. p. 608), and by the foremost part of the parasphenoid (*Psph*, figs. 37, 44, 50, 55, 56, 62 B, 64 A, 65 A, 74, 75, 76 B, C, 81, 83 B, 87 A; pl. 3, figs. 1, 2; pl. 4, fig. 1; pl. 5, fig. 2; pl. 8, fig. 1;

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[1] The bones in Postdevonian Coelacanthids described as postrostrals by Stensiö (1921, p. 124; figs. 21, 43, 51; 1932, figs. 15, 18), Moy-Thomas (1935 a; 1937), Nielsen (1936), and others must now be regarded as nasals. The same presumably applies also to the large "postrostrals" in *Dictyonosteus* (cf. Stensiö 1921, fig. 58; 1922 a, fig. 3 and p. 580 below).

pl. 12, figs. 3—6; pl. 13; pl. 15, fig. 1; pl. 17, figs. 1, 2). Besides these two bones, we find in *Eusthenopteron* and *Holoptychius* on the lower side of the ethmoidal region also a palatal lamina (*la. pal*, figs. 36 A, 53 56, 58) which is formed by the dermal bones of the ethmoidal shield and which covers a marginal zone of the lower face of the region. In the formation of this lamina participate in *Eusthenopteron* (figs. 52 B; 53, 56, 58; p. 450; cf. *Porolepis*, pl. 3, fig. 3), on either side of the median line, the pars palatina (Pmx_3) of the premaxillary proper and the palatal processes of the medial and lateral rostrals (*R. m. pal*, *R. l. pal*) dorsally to that part.

Finally also the dermopalatine, though belonging to the palatoquadrate-cheek complex, extends forwards into the snout. In *Eustenopteron* this bone (*Dpl*, *la. Dpl*, figs. 55, 56, 60, 64 A, 65 A, 87 A; pl. 8, fig. 1, pl. 10; pl. 12, figs. 3—6; pl. 13; pp. 453—454) runs forward somewhat underneath the ethmoidal region. In *Porolepiformes* it has so far not been found preserved. In *Latimeria* (*37″*, fig. 83 B) it seems to be represented by the "autopalatine dental plate" (bone *37″* of SMITH's description). The bone termed by SMITH (1939, p. 69; *53″*, fig. 10) the "dental plate of the prevomer" is a predermopalatine, a bone, which has no equivalent in Rhipidistid Crossopterygians (see p. 608).

Summing up the main points of what has been set forth above, we find the following. 1) The sensory canals of the snout in primitive representatives of all three groups have a very similar course and their disposition is very simple. 2) In certain later *Osteolepiformes*, but above all in the Postdevonian *Coelacanthiformes*, there arise sensory canal commissures giving the sensory canals a complicated disposition. As they are absent or but slightly developed in primitive forms, these commissures at least partly are secondary formations (cf. pp. 602, 618; foot-note 1 on p. 605). 3) Presuming that the new interpretation of the dermal bones of the snout in Coelacanthids is true, the dermal bones of the snout have a fundamentally similar disposition in all the main groups of Crossopterygians.

As regards the detailed development of the dermal bones of the snout, there are several differences between the three groups of Crossopterygians. The most important ones will be treated below (pp. 490—493, 595).

B. The Snout in Porolepiformes.

1. Descriptive section.

a. Genus Porolepis Woodward.

(Figs. 36—43, 46 A; pls. 1—5; pl. 6, fig. 3).

Previous investigations. — The snout in *Porolepis* has been but slightly known. A few superficial comments on it were made in 1922

(STENSIÖ 1922 a, p. 1259; pl. 1, fig. 5). Since then a few figures have been published (SÄVE-SÖDERBERGH 1932 a, pp. 91—92, fig. 17; STENSIÖ 1932, fig. 30; HOLMGREN and STENSIÖ 1936, fig. 271). These figures show that the nasal capsule has a decided lateral position in the ethmoidal region and that it is separated from the corresponding capsule of the opposite side by a paired, wide and deep fossa opening ventrally and assumed to have been developed for one or a few of the large anterior teeth of the lower jaw (HOLMGREN and STENSIÖ 1936, p. 347). The figures in question also demonstrate that the nasal cavity opens outwards through two external apertures and downwards into the mouth through an internal nasal aperture.

Material. — The subsequent account of the anterior parts of the endocranium in *Porolepis* is based above all on the holotype of *P. spitsbergensis* n. sp.[1] which is from the Lower Devonian (the Wood Bay Series) at Wood Bay, Spitzbergen, and belongs to the Palaeontological Museum of the University of Oslo. This holotype (pl. 1; pl. 2, figs. 2, 3) consists of a well-preserved divisio cranialis anterior lacking a large posterior ventro-medial endocranial part, the parasphenoid, the vomers, and the entire right side as far as to the medial wall of the right nasal cavity. It is split in such a way as to enable a detailed examination of the left nasal cavity and the medial parts of the cast of this cavity.

A number of other specimens from the Lower Devonian of Spitzbergen have also been studied. These specimens (pl. 2, fig. 1; pls. 3—5; pl. 6, fig. 3) were all collected by the English-Norwegian-Swedish Spitzbergen expedition in 1939.[2] In the structure of the snout they agree essentially with *P. spitsbergensis*. They have preliminarily been referred to the genus *Porolepis* which is represented in the Lower Devonian of Spitzbergen not only by *P. spitsbergensis*, but also by two other species *P. brevis* n. sp. and *P. elongata* n. sp.[1] The differences between the three species refer mainly to the proportions and certain minor details and have no bearing on the anatomy of the snout as discussed below.[3]

Description. — As in other Devonian Crossopterygians, the endocranium in *Porolepis* is occupied by two large unpaired ossifications, an anterior one, the ethmosphenoid, and a posterior one, the oticooccipital.

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[1] Diagnosis of the new *Porolepis* species will be given in a future work.

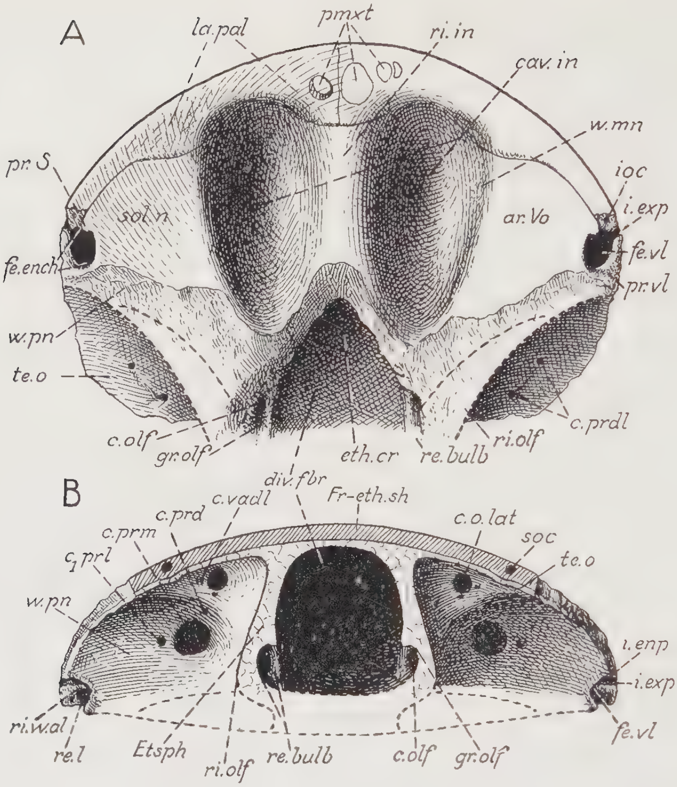
[2] They belong to the British Museum of Natural History in London, the Palaeontological Museum of the University of Oslo, and the Swedish Museum of Natural History in Stockholm. Owing to the war they have not yet been divided among the three museums.

[3] It is possible that they belong to different genera but for practical reasons they have provisionally been included in the same genus.

The ethmoidal region, the posterior boundary of which is here considered to be the transverse plane through the posterior orifice of the medial profundus canal (*c.prm*, figs. 36 B, 37 B, 38 A, 42; cf. fig. 43), is completely ossified and formed throughout by the anterior and broad part of the ethmosphenoid. As the other regions of the endocranium, it consists of cancellated bony tissue lined with a thin periostal bone layer on the outside and in all cavities and canals. The cancellated bony tissue is well preserved in certain specimens, whereas it is more or less absent in others.

The ethmoidal region covers a good third of the length of the ethmosphenoid ossification and may be characterized as broad and low. It is highest in its hindmost median part, whence it decreases in height forwards and towards the sides, and is broadest about at the transition between its middle and posterior thirds. The relative proportions between its breadth, length and height in *P. brevis* are about 10:5:4.

The ethmoidal region presents a strongly arched dorsal face, a ventral face, and a paired posterior face. All these three faces meet ventrolaterally on either side at an obtuse corner, the ventro-lateral corner. At this corner we find a somewhat irregularly shaped opening, the fenestra ventro-lateralis (*fe.vl*, figs. 36, 37 A, 39 B, 40), which leads to the nasal cavity. Immediately laterally to this fenestra the postnasal wall (*w.pn*, figs. 36, 37 A, B, 39 B, 43) forms a small process pointing ventrally, the processus ventro-lateralis (*pr.vl*, figs. 36 A, 37, 40). The internasal wall (*w.in*, figs. 39 B, 43) is very broad. The hinder division of this wall houses the foremost part of the cranial cavity, the ethmoidal part of the cranial cavity (*eth.cr*, figs. 36 A, 38, 43). In the anterior parts of this wall there is a paired, large and deep cavity opening ventrally, the cavum internasale (*cav.in*, figs. 36 A, 37 A, 39 A, 43), which is separated from the corresponding cavity of the opposite side by a strong median ridge, the internasal ridge (*ri.in*). The cavum internasale extends forwards from the internasal wall into the comparatively short and broad divisio prenasalis communis (*w.pren*, figs. 43, 46 A) and thus its anterior part actually represents a cavum prenasale. However, as it is fairly inconsiderable, this anterior part developed in the divisio prenasalis communis has not been distinguished from the cavum internasale proper. The nasal cavity (*cav.nc*, figs. 38 A, 39; see also figs. 42, 43) of either side occupies only a comparatively small lateral part of the ethmoidal region and thus lies far from that of the opposite side. Its walls are unusually complete, being pierced by canals for vessels and nerves and by the small fenestra endonarina anterior (*fe.ena*, figs. 39 A, 40 A, C, 43, 46 A) and the fenestra ventro-lateralis only. The latter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B
c.vadl
Fr-eth.sh
c.prd
c.o.lat
c.prm
soc
$c_1$prl
te.o
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i.enp
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ri.w.al
fe.vl
re.l
Etsph
ri.olf
re.bulb
c.olf
gr.olf

Fig. 36. *Porolepis spitsbergensis* Jarvik. Imperfect anterior part of the divisio cranialis anterior. *A*, in ventral, and *B*, in posterior view. Postero-medial parts of the endocranium, the parasphenoid and the vomers missing. Holotype, partly restored. Sutures between the dermal bones of the fronto-ethmoidal shield omitted. $^{3}/_{2}$.

Etsph, ethmosphenoid; *Fr-eth. sh*, fronto-ethmoidal shield; *ar. Vo*, vomeral area; *cav. in*, cavum internasale; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. prd*, *c. prdl*, canals, probably for dorsal and dorso-lateral branches of n. profundus; *c. prm*, medial profundus canal; *c. vadl*, canal directed dorso-laterally, probably mainly for vessels; c_1 *prl*, lateral profundus canal; *div. fbr*, forebrain division of cranial cavity; *eth. cr*, ethmoidal part of cranial cavity; *fe. ench*, ventro-medial division of fenestra ventrolateralis, representing fenestra endochoanalis; *fe. vl*, fenestra ventro-lateralis; *gr. olf*, groove for n. olfactorius; *i. enp*, notch in the margin of fenestra ventro-lateralis for posterior nasal tube; *i. exp*, notch in the margin of ethmoidal shield for posterior nasal tube; *ioc*, infraorbital sensory canal; *la. pal*, lamina palatina of ethmoidal shield; *pmxt*, premaxillary teeth; *pr. S*, Seydel's palatal process; *pr. vl*, ventro-lateral process of postnasal wall; *re. bulb*, recess for bulbus olfactorius; *re. l*, lateral recess of nasal cavity; *ri. in*, internasal ridge; *ri. olf*, olfactory ridge; *ri. w. al*, crista rostro-caudalis; *soc*, supraorbital sensory canal; *sol. n*, solum nasi; *te. o*, tectum orbitale; *w. mn*, medial nasal wall; *w. pn*, postnasal wall.

fenestra consists of two divisions, a dorso-lateral one, the fenestra endonarina posterior (*fe. enp*, figs. 39 B, 40 A, C, 42 B, C, E), and a ventro-medial one, the fenestra endochoanalis (*fe. ench*, figs. 36 A, 39 B, 40 D, 42 B, E, 46 A). In the nasal cavity we may distinguish a principal chamber and a comparatively weakly developed lateral recess (*re. l*, figs. 36 B, 37 B, 39, 40 A, C, 42 A, B, C) which is bounded off dorsally from the principal cavity by a longitudinal crest, the crista rostro-caudalis (*ri. w. al*), situated on the medial (internal) face of the lateral nasal wall.

The foremost part of the orbitotemporal region (figs. 36, 37, 43) includes an anterior portion of the interorbital wall (*w. io*) and the anterior part of a fairly complete orbital roof, the tectum orbitale (*te. o*).

The foremost part of the palatoquadrate, the pars autopalatina, is strongly developed and well ossified. As it has been found preserved only in one single specimen, where it is much crushed and damaged, it will not be bescribed here (cf. pp. 386—387, 412).

We shall now proceed to a detailed description of the anterior parts of the endocranium. As far as the material available permits this description will be made fairly exhaustive. We shall first turn to the principal external faces.

The dorsal face of the ethmoidal region (figs. 39, 40 A, C, 43, 46 A; pl. 1, fig. 2; pl. 3; fig. 3; pl. 4, fig. 2) is covered by the ethmoidal shield in all the specimens examined. It could thus be examined in fracture sections only and in the places where the overlying dermal bones were worn off, and cannot be completely described. As it is not separated by any interspace from the dermal bones above it, it is obvious, however, that its main features on the whole resemble the external face of the ethmoidal shield (figs. 37 B, C, 40 B, 41, 46 A; pl. 1, figs. 2, 3; pl. 2, fig. 1; pl. 3, fig. 3; pl. 4, fig. 2). It thus slopes both forwards and towards the sides. It presents a paired rostro-caudal groove (*gr. soc*, figs. 39, 43), which is occupied by the ridge on the lower side of the fronto-ethmoidal shield (fig. 46 A; cf. fig. 1, *ri. soc*) that houses the supraorbital sensory canal. This groove, exposed only in certain specimens of *P. elongata* and *P. brevis*, is traceable backwards also on to the dorsal face of the tectum orbitale (fig. 37 B). It accurately reflects the course of the supraorbital sensory canal. During its passage forwards it makes first a lateral and then, further anteriorly, a medial bend. The latter bend, more distinct than the posterior one, is approximately above the transition between the tectum nasi, which bulges somewhat upwards, and the internasal wall. The foremost part of the groove goes in a ventral and somewhat lateral direction down to the very margin between the face now under consideration and the ventral face, there forming a shallow notch. The part of the tip of the ethmoidal region situated medially to this notch, between it and the corresponding notch of the opposite side, is in fact a short and broad rostral process. As the ethmoidal commissure of the infraorbital sensory canals is situated ventrally to it (cf. pp. 334—335), this process must be interpreted as a dorsal rostral process (cf. p. 258). Both the fenestra endonarina anterior and the fenestra endonarina posterior are found on the dorsal face of the ethmoidal region. The former of these fenestrae (pp. 369—370) lies comparatively far forwards and dorsally, whereas the latter (see p. 371) which, as already mentioned, forms the dorso-lateral division of the fenestra ventro-lateralis, is situated at the very ventro-lateral corner of the face. Besides the two openings just mentioned, the face also displays several small foramina which are the upper orifices of fine canals (*c. prt*, c_1*prdm*, c_2*prdm*; pp. 373, 375) ascending through the tectum nasi. The approximate position of these foramina is seen in fig. 43, which also shows the dorsal openings of the canals (*c. prdl*, *c. vadl*) that pierce the anterior part of the tectum orbitale (pp. 372, 373). No canals could be observed for the lateralis branches to the sensory organs (neuromasts) of the supraorbital sensory canal.

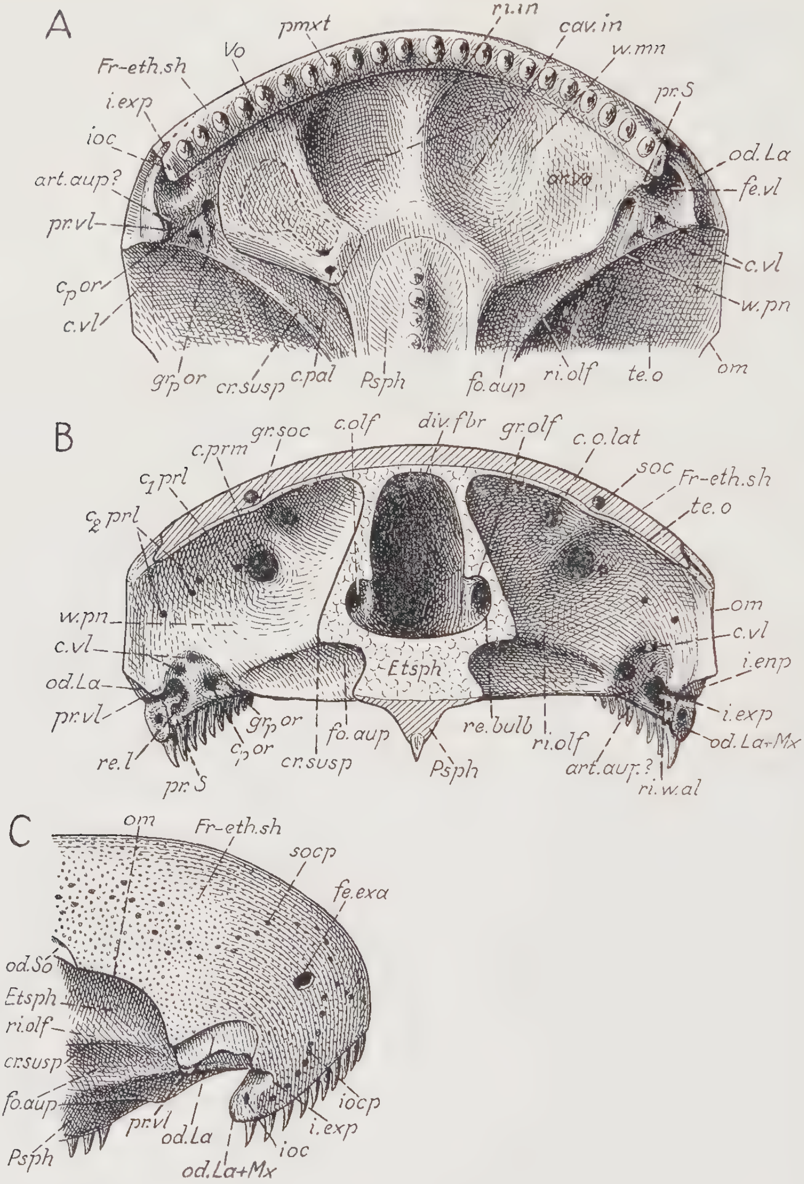
The ventral face of the ethmoidal region (figs. 36 A, 37 A, 39, 40 A, B, D, 46 A; pl. 1, fig. 1; pl. 2, figs. 2, 3; pl. 3, fig. 2; pl. 4, fig. 2; pl. 5) is well preserved, but is not fully exposed, being covered to some extent by dermal bones in all the specimens at my disposal. It is thus covered anteriorly and laterally on a narrow marginal zone by the palatal lamina (*la. pal*) of the ethmoidal shield and most posteriorly on a median area by the foremost part of the broad parasphenoid (*Psph*). The paired vomer, on the other hand, is generally lacking and is found in position only on one side in a single specimen of *P.* cf. *brevis* (*Vo*, fig. 37 A; pl. 5, fig. 2).

Judging from what is now known concerning the cranium as a whole, the ventral face of the ethmoidal region must have been directed ventrally and somewhat anteriorly. Posteriorly it passes over into the comparatively narrow ventral face of the interorbital wall. The last-mentioned face was also directed ventrally and somewhat anteriorly as far backwards as to the posterior end of the parasphenoid, whereas its hindmost parts, behind the parasphenoid, are horizontal. Accordingly the anterior and posterior parts of the ventral face of the ethmosphenoid meet at an obtuse angle behind the parasphenoid, an angle (pl. 4, fig. 2) which in position as well as appearance reminds of the basal angle of the Selachians.

The medial parts of the ventral face of the ethmoidal region are entirely occupied by the large openings of the cavum internasale (p. 364). Postero-laterally to this opening on either side lies the fairly plane vomeral area (*ar. Vo*, figs. 36 A, 37 A; pl. 2, figs. 2, 3; pl. 3, fig. 2; pl. 4, fig. 1; pl. 5) which is covered by the vomer and which constitutes the ventral face of the solum nasi (*sol. n*). This area is fairly narrow postero-medially towards the median area covered by the parasphenoid (*Psph*, fig. 37; pl. 3, fig. 1; pl. 4, fig. 1; pl. 5, fig. 2) but widens somewhat antero-laterally, where, anteriorly to the fenestra ventro-lateralis, it is continuous with the narrow marginal zone which is covered by the palatal lamina of the ethmoidal shield (*la.pal*, fig. 36 A; pl. 2, fig. 3; pl. 6, fig. 3; *R.l.pal*, Pmx_3, pl. 3, fig. 3; cf. p. 450). This narrow marginal zone stretches along the whole anterior end of the ethmoidal region backwards to the fenestra ventro-lateralis of either side.

The postero-lateral corner of the ventral face of the ethmoidal region forms a small, triangular and somewhat depressed area, which lies behind the lateral half of the vomeral area (*ar. Vo*) and the fenestra ventrolateralis and in the main on the latero-ventral part of the postnasal wall. This area faces downwards and fairly much backwards, but is rather variable as to its detailed development. It is not preserved in the holotype of *P. spitsbergensis*, while it is quite evident in several specimens of both *P. brevis* and *P. elongata*. On its medial part close to the vomeral area (*ar. Vo*), there is a more or less distinct groove, $gr_{p}or$ (figs. 37 A, B, 40 A, B, D; pl. 3, figs. 1, 2; pl. 4, fig. 1; pl. 5), which runs forwards and somewhat laterally from the posterior margin of the area. During its passage forwards this groove increases gradually in depth. It leads to the posterior opening of a canal, $c_{p}or$ (figs. 37 A, B, 39 B, 40 D, 42 B, C, E; pl. 3, figs. 1, 2; pl. 4, fig. 1; pl. 5; pl. 6, fig. 3), which pierces the solum nasi at the transition to the postnasal wall. The groove $gr_{p}or$ and the canal $c_{p}or$ form together the posterior part of a passage for nerves and vessels, the orbitorostral passage, to be described below (pp. 369, 375). The lateralmost part of the triangular depressed area presents a more or less distinct pit, and immediately laterally to this, on the medial side of the processus ventro-lateralis (*pr.vl*), a small facet directed postero-ventro-medially. The position of this pit and facet (*art.aup*?, figs. 37 A, B, 40 D; pl. 3, figs. 1, 2; pl. 4, fig. 1; pl. 5, fig. 1) are such that they may be supposed to form an articular area for the antero-lateral part of the pars autopalatina palatoquadrati. Between this presumed articular area and the posterior part of the groove $gr_{p}or$ we find a short groove which from the orbit runs forwards and slightly laterally to a fine canal (*c.vl*, figs. 37 A, B, 40 A, D, 42 A, C, E; pl. 3, figs. 1, 2; pl. 4, fig. 1; pl. 5). This canal pierces the ventrolateral part of the postnasal wall and seems to enter the nasal cavity. In one single specimen of *P. brevis* there is a double canal on one side (fig. 37 A, B; pl. 3, fig. 1; pl. 4, fig. 1).

The posterior paired face of the ethmoidal region (figs. 36 B, 37 B, 43; pl. 1, figs. 3, 4; pl. 2, fig. 2; pl. 3, fig. 1), that is to say the orbital face of the postnasal wall, is high medially, where it is continuous


A
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gr_p or
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cr.susp
fo.aup
Etsph
Psph
re.bulb
ri.olf
art.aup.?
ri.w.al
od.La+Mx
i.exp
i.enp
c.vl
om
C
om
Fr-eth.sh
socp
fe.exa
od.So
Etsph
ri.olf
cr.susp
fo.aup
Psph
pr.vl
od.La
od.La+Mx
ioc
i.exp
iocp

Fig. 37. *Porolepis brevis* Jarvik. Restoration of the anterior part of the divisio cranialis anterior. *A* ventral, *B* posterior, *C* lateral aspects. Mainly after specimen E.-N.-S. (English-Norwegian-Swedish Spitzbergen expedition in 1939), No. 214. Sutures between the dermal bones of the fronto-ethmoidal shield omitted. $^8/_1$.

Etsph, ethmosphenoid; *Fr-eth. sh*, fronto-ethmoidal shield; *Psph*, parasphenoid; *Vo*, vomer; *art. aup?*, area against which pars autopalatina probably abutted; *ar. Vo*, vomeral area; *cav. in*, cavum internasale; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; $c_p or$, posterior canal of orbitorostral passage; *c. pal*, canal for r. palatinus VII; *c. prm*, medial profundus canal; *cr. susp*, crista suspendens; *c. vl*, canal piercing the with the interorbital wall, but decreases in height laterally and is lowest in its lateral parts. At the ventro-lateral corner of this face behind the fenestra ventro-lateralis the postnasal wall is produced downwards into the small obtuse processus ventro-lateralis already referred to above (*pr. vl*, figs. 36 A, 37, 40; pl. 1, figs. 3, 4; pl. 2, figs. 1, 3; pl. 3, figs. 1, 2; pls. 4, 5). The lateral side of that process is covered almost entirely by a part of the ethmoidal shield that is overlapped by the lachrymal (*od. La*, figs. 37, 40 B; pl, 1, fig. 3; pl. 2, fig. 1; pl. 3, figs. 2, 3; pl. 4). On its medial side is the facet *art. aup*? referred to above.

On the medial lower part of the posterior face of the ethmoidal region we find a strong and mainly horizontal ridge, the olfactory ridge (*ri. olf*, figs. 36, 37; pl. 3, figs. 1, 2; pls. 4, 5), within which passes the canalis olfactorius. This ridge begins posteriorly on the lateral face of the interorbital wall immediately antero-ventrally to the external opening of the opticus canal (*c. II*, fig. 38 B) and goes from there forwards onto the ethmoidal region. At the transition to that region it is still fairly pronounced and bears a sharp crest, directed downwards, the crista suspendens (*cr. susp*, fig. 37; pl. 3, figs. 1, 2; pls. 4, 5), but then decreases rapidly in height on the posterior face of the ethmoidal region and finally disappears before reaching the lateralmost part of that face. Ventrally to the olfactory ridge there is a long, large and distinct fossa, the autopalatine fossa (*fo. aup*, fig. 37; pl. 3, figs. 1, 2; pls. 4, 5), which from the hinder part of the orbitotemporal region stretches forwards onto the ethmoidal region and is so situated as undoubtedly to have been developed for the articulation of the antero-medial part of the palatoquadrate. The fossa is distinctly bounded dorsally and dorso-laterally by the olfactory ridge and the crista suspendens, and ventrally by a narrow ledge formed by the ventral margin of the postnasal wall and the ventral margin of the interorbital wall. The ventral ledge is continuous posteriorly with the lowermost part of the basipterygoid process (*pr. bp*, pl. 3, figs. 1, 2; pl. 4; pl. 5, fig. 2),

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ventro-lateral part of postnasal wall; c_1 *prl*, c_2 *prl*, lateral profundus canals; *div. fbr*, forebrain division of cranial cavity; *fe. exa*, fenestra exonarina anterior; *fe. vl*, fenestra ventro-lateralis; *fo. aup*, autopalatine fossa; *gr. olf*, groove for n. olfactorius; gr_p*or*, posterior groove of orbitorostral passage; *gr. soc*, groove for ridge containing supraorbital sensory canal; *i. enp*, notch in the margin of fenestra ventro-lateralis for posterior nasal tube; *i. exp*, notch in the margin of ethmoidal shield for posterior nasal tube; *ioc*, infraorbital sensory canal; *iocp*, pores of infraorbital canal; *od. La*, area of ethmoidal shield overlapped by lachrymal; *od. La + Mx*, area of ethmoidal shield overlapped by lachrymal and maxillary; *od. So*, area of fronto-ethmoidal shield overlapped by supraorbital; *om*, margin of orbital opening; *pmxt*, premaxillary tooth; *pr. S*, Seydel's palatal process; *pr. vl*, ventro-lateral process of postnasal wall; *re. bulb*, recess for bulbus olfactorius; *re. l*, lateral recess of nasal cavity; *ri. in*, internasal ridge; *ri. olf*, olfactory ridge; *ri. w. al*, crista rostro-caudalis; *soc*, supraorbital sensory canal; *socp*, pores of supraorbital canal; *te. o*, tectum orbitale; *w. mn*, medial nasal wall; *w. pn*, postnasal wall.

and as it increases in breadth posteriorly it forms a narrow subocular shelf in front of the basipterygoid process.

The posterior face of the ethmoidal region presents several foramina. On its upper middle part is the posterior orifice of a wide canal, the medial profundus canal (*c. prm*, figs. 36 B, 37 B; see p. 373), which runs forwards to the nasal cavity. Laterally to the orifice *c. prm* there are one or more small foramina with somewhat varying positions. At least the majority of these small foramina are the posterior openings of fine canals, the lateral profundus canals (c_1*prl*, c_2*prl*, figs. 36 B, 37 B; see p. 375). Dorso-medially to the posterior orifice of the medial profundus canal (*c. prm*) the postnasal wall, at its transition into the antero-dorso-lateral part of the interorbital wall, suddenly greatly increases in thickness and bears a more or less pronounced oblique ridge which passes from above and laterally in a direction downwards and medially. Immediately dorso-medially to this oblique ridge, and close below the tectum orbitale, lies the posterior opening of the canal (*c. o. lat*, figs. 36 B, 37 B; pl. 1, figs. 3, 4; pl. 3, fig. 1; pl. 4, fig. 1; pl. 5, fig. 1) for the r. ophthalmicus lateralis. In *P. spitsbergensis* this opening is situated in a deep fossa (fig. 36 B; pl. 1, fig. 4) in which three other openings are also to be noticed, two lateral ones (*c. vadl*) and one ventral one (*c. prd*). From the latter opening a canal (*c. prd*) descends almost vertically, pierces the oblique ridge mentioned above, and opens ventrally a little dorso-medially and posteriorly to the orbital orifice of the medial profundus canal.

The division of the cranial cavity situated within the ethmosphenoid bone (*cav. cr*, *eth. cr*, *div. fbr*, figs. 36, 37 B, 38, 43; pl. 1, figs. 1, 4; pl. 2, fig. 3; pl. 3, fig. 1; pl. 5, fig. 1) could be examined fairly thoroughly. It has a very thin roof, situated immediately underneath the dermal skull-roof, thin lateral walls, but a thick floor. Most posteriorly it is comparatively low and narrow (pl. 3, fig. 1; pl. 5, fig. 1), but a little further forwards where we find the deep fossa hypophyseos (*fo. hyp*, fig. 38 B) it is higher. Still further forwards it is much wider. Throughout its long anterior part it is comparatively high and broad. This high and broad part (*div. fbr*, figs. 36, 37 B, 38; pl. 1, figs. 1, 4; pl. 2; fig. 3; pl. 5, fig. 1) which in the main housed the forebrain, may be termed the forebrain division. The posterior part of its roof is pierced by an opening above which there is a pit (cf. fig. 33, *fo. pin*) on the lower side of the dermal skull-roof. This opening and pit together form a dorsal median recess, the recessus pinealis (*re. pin*, fig. 38; pl. 5, fig. 1), which must have been developed for the pineal organ. In some of the specimens there is also an opening in the dermal skull-roof above the recess just described, but whether this opening is a real pineal foramen or an artifact could not be ascertained. Postero-ventrally on either side the hindmost part of the forebrain division presents a well pronounced lateral recess (*re. bulb*, figs. 36, 37 B, 38; pl. 1, figs. 1, 4; pl. 2, fig. 3; pl. 5, fig. 1) which lies in the posterior part of the olfactory ridge (*ri. olf*) and in all probability housed the bulbus olfactorius. The anterior part of the roof of this recess is deeply grooved (*gr. olf*, figs. 36, 37 B, 38; pl. 1, fig. 1; pl. 2, fig. 3) and bounded medially by a crest descending from the medial side of the lateral wall of the cranial cavity. The groove runs forwards and slightly laterally and about at the transition between the orbitotemporal and ethmoidal regions it passes over into the fairly short and wide canalis olfactorius (*c. olf*, figs. 36, 37 B, 38, 39 B, 42, 43; pl. 1, figs 1, 2, 4; pl. 2, fig. 3). The forebrain division of the cranial cavity, however, goes quite far forwards in front of the posterior opening of the canalis olfactorius and this foremost portion constitutes the ethmoidal part (*eth. cr*, figs. 36 A, 38, 43; pl. 1, fig. 1; pl. 2, fig. 3; pl. 5, fig. 1) of the cranial cavity already referred to. More precisely the ethmoidal part of the cranial cavity lies in the hinder part of the internasal wall in which it goes forwards in the internasal ridge (*ri. in*; see pp. 365—366) as far as to a transverse plane through the fenestra ventro-lateralis. Though narrowing and decreasing somewhat in height anteriorly it is nevertheless fairly broad and high at its an-

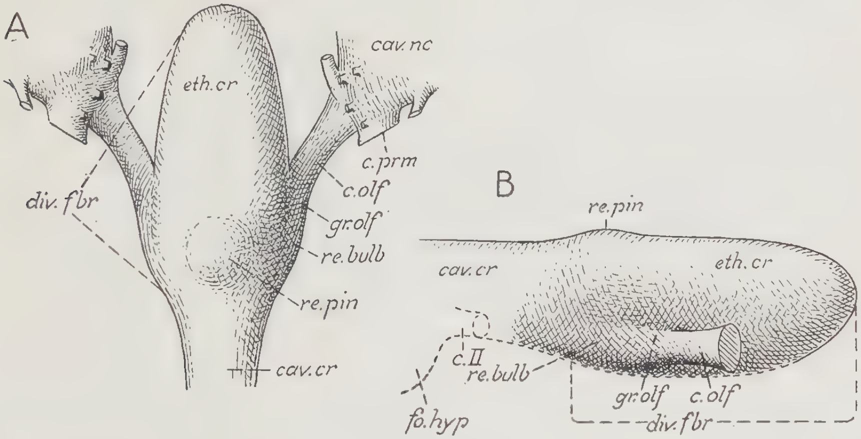

Fig. 38. *Porolepis.* Restoration of the cast of the anterior part of the cranial cavity and the canales olfactorii. *A*, dorsal, and *B*, lateral view. Mainly from the holotype of *Porolepis spitsbergensis*, but certain particulars from *P. elongata* specimen No. 229 collected by the English-Norwegian-Swedish Spitzbergen expedition in 1939; (pl. 5, fig. 1). $^3/_2$ approximately.

cav. cr, cranial cavity (diencephalic division); *cav. nc*, cavity of nasal capsule; *c. olf*, canalis olfactorius; *c. prm*, medial profundus canal; *c. II*, opticus canal; *div. fbr*, forebrain division of cranial cavity; *eth. cr*, ethmoidal part of cranial cavity; *fo. hyp*, fossa hypophyseos; *gr. olf*, groove for n. olfactorius; *re. bulb*, recess for bulbus olfactorius; *re. pin*, recess for pineal organ.

terior end. Its decreasing height towards that end is produced by a raising of the floor. Its roof is thin and lies in the straight anterior extension of the roof of the orbitotemporal region. Its anterior boundary is formed by the solid anterior part of the internasal ridge (*ri. in*) and its lateral boundary by the hinder thin part of the internasal ridge anteriorly and by the postnasal wall posteriorly (fig. 43). Finally, its floor, also formed by the internasal ridge, is fairly thick and passes over posteriorly into the ventral wall of the orbitotemporal region.

From the shape of the cranial cavity it is possible to draw certain conclusions concerning the general character of the anterior principal divisions of the brain in *Porolepis* (fig. 43; cf. pp. 384—385).

The forebrain, which occupied the forebrain division of the cranial cavity, was considerably broader posteriorly than the diencephalon. The two hemispheres (*hem*, fig. 43) were oblong and narrower and lower anteriorly than posteriorly. They must have lain close to one another, but whether they were separated medially by a median groove or fissure (fissura sagittalis) could not be ascertained. The lateral recess (*re. bulb*) has such a position and such relations to the canalis olfactorius that it must be assumed to have lodged the bulbus olfactorius (*b. olf*) of its side. The bulbus olfactorius thus lay, in all probability, ventro-laterally to the posterior part of the hemisphere of its side and was continuous with it only ventrally. Dorsally it was separated from the hemisphere by a distinct rostro-caudal groove. Anteriorly the bulbus passed over into the olfactory nerve (*I*) which went forwards to the nasal cavity through the canalis olfactorius. The fact that the canalis olfactorius opens anteriorly with a widened funnel-like aperture may possibly indicate that at its entrance into the nasal cavity the n. olfactorius divided into several fine branches very much in the manner shown diagrammatically in fig. 43.

The cavum internasale (*cav. in*, figs. 36 A, 37 A, 39, 43, 46 A; pl. 1, fig. 1; pl. 2, fig. 3; pl. 3, fig. 2; pl. 4, fig. 1; pl. 5) is, as we have seen, a large paired cavity separated from that of the opposite side by the strong median internasal ridge (*ri. in*). It is situated in the anterior parts of the internasal wall mainly in front of the ethmoidal part of the cranial cavity, but as has been stressed above (p. 355) it extends forwards also a little into the divisio prenasalis communis so as actually to include a small cavum prenasale. Its large paired ventral opening is situated on the medial part of the lower face of the ethmoidal region. Viewed from below each cavum appears as a marked fossa or deep depression which is always longer than broad. Its size and depth are fairly different in different species. In *P. spitsbergensis* it is thus both very long and very deep (figs. 36 A, 39; pl. 1, fig. 1; pl. 2, fig. 3). In

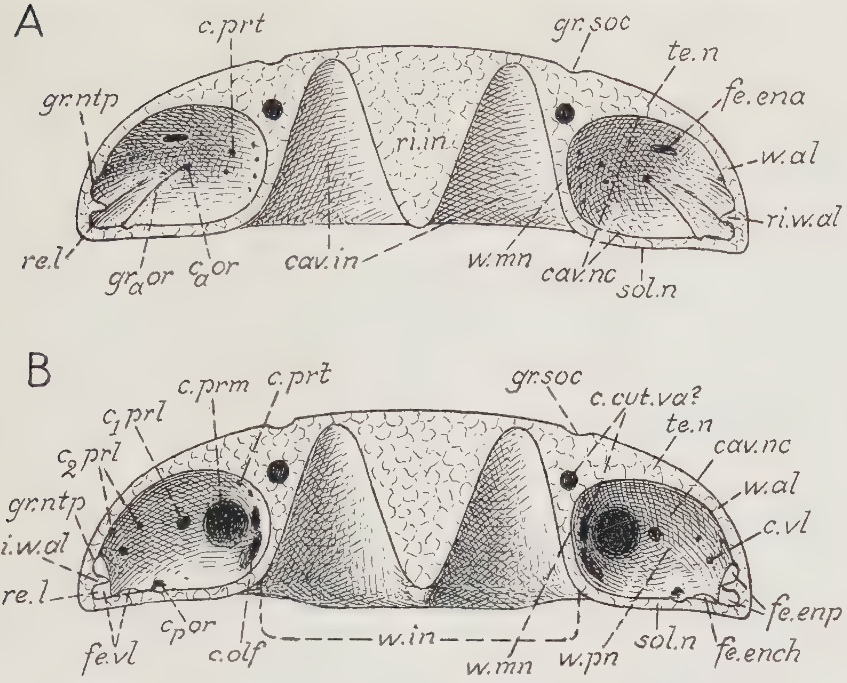

Fig. 39. *Porolepis spitsbergensis* Jarvik. Restoration of the ethmoidal region of the endocranium. *A*, anterior half in posterior view. *B*, posterior half in anterior view. A few particulars after specimens of *Porolepis brevis*. Cross-sections through bony tissue reticulated. $^2/_1$.

$c_a or$, anterior canal of orbitorostral passage; *cav. in*, cavum internasale; *cav. nc*, cavity of nasal capsule; *c. cut. va?*, canal for branch of n. profundus but possibly also for cutaneous vessel; *c. olf*, canalis olfactorius; *c. prm*, medial profundus canal; $c_p or$, posterior canal of orbitorostral passage; *c. prt*, canal for terminal twig of medial terminal profundus branch; *c. vl*, canal piercing ventro-lateral part of postnasal wall; $c_1 prl$, $c_2 prl$, lateral profundus canals; *fe. ena*, fenestra endonarina anterior; *fe. ench*, ventro-medial division of fenestra ventro-lateralis, representing fenestra endochoanalis; *fe. enp*, dorso-lateral division of fenestra ventro-lateralis, representing fenestra endonarina posterior; *fe. vl*, fenestra ventrolateralis; $gr_a or$, anterior groove of orbitorostral passage; *gr. ntp*, groove for posterior nasal tube; *gr. soc*, groove for ridge housing supraorbital sensory canal; *re. l*, lateral recess of nasal cavity; *ri. in*, internasal ridge; *ri. w. al*, crista rostro-caudalis; *sol. n*, solum nasi; *te. n*, tectum nasi; *w. al*, (antero-)lateral nasal wall; *w. in*, internasal wall; *w. mn*, medial nasal wall; *w. pn*, postnasal wall.

this species it is deepest in its anterior half where it extends upwards almost to the ethmoidal shield, from which it is separated by a thin layer of cartilage-bone only (fig. 39; cf. fig. 46). On the other hand, it is shorter and much shallower both in *P. brevis* (fig. 37 A; pl. 3, fig. 2; pl. 4, fig. 1; pl. 5, fig. 2) and *P. elongata* (pl. 5, fig. 1). The internasal ridge (*ri. in*) has an anterior part (figs. 36 A, 37 A, 39, 43, 46 A) forming a solid septum which broadens forwards and is continuous anteriorly with the divisio prenasalis communis. Its posterior part, which increases considerably in width backwards, is hollow and houses the ethmoidal part of the cranial cavity (*eth. cr*; see figs. 36 A, 43; pl. 1, fig. 1; pl. 2, fig. 3; pl. 5, fig. 1). Its latero-ventral portion on either side, which is continuous with the postnasal wall of the same side, is developed only as a thin wall between the ethmoidal part of the cranial cavity and the cavum internasale. The median ventral portion of the posterior part of the ridge forms the floor of the ethmoidal part of the cranial cavity (cf. p. 364). The cavum internasale is bounded anteriorly and antero-laterally by the divisio prenasalis communis and further backwards on its lateral side by the anterior part of the medial nasal wall (*w. mn*, figs. 36 A, 37 A, 39, 43; cf. p. 367). The last-mentioned wall, which is thin, is not quite sagittal in position, but converges somewhat backwards towards the median line of the skull. Owing to this position of the wall in question the cavum internasale decreases somewhat in breadth backwards.

According to STENSIÖ (1932, p. 81, fig. 30; cf. HOLMGREN and STENSIÖ 1936, p. 347) the deep fossa here described as the cavum internasale was developed for one or more of the large anterior coronoid tusks of the lower jaw. On the basis of the new *Porolepis* material now available and in the light of our present knowledge of the *Porolepiformes* a new and more satisfactory explanation of the function of the cavum internasale can be given. The material of Crossopterygians at my disposal from the Lower Devonian of Spitzbergen includes inter alia a well-preserved lower jaw conceivably of *Porolepis* (cf. GROSS 1941, fig. 23) which is of interest in this connection. This lower jaw was provided with three pairs of coronoid tusks all of which are fairly small and so short that their points hardly reach above the labial margin of the dentary. The foremost of them is situated far behind the anterior end of the lower jaw. Owing to this and to its small size it cannot possibly have extended into the cavum internasale when the mouth was shut. In *Eusthenopteron* (cf. JARVIK 1937, figs. 8, 9, 15—17) the foremost large coronoid tusk lies, when the mouth is shut, close to the corresponding vomerine tusk (*vot*, figs 50, 56, 87 A; pl. 8, fig. 1), but despite the fact that it is longer than the corresponding one in *Porolepis*, it did not cause the formation of a pit or fossa in or through the vomer. In a specimen of an undetermined *Holoptychius* species from East Greenland (fig. 44) the tusk of the vomer (*vot*) is not nearly so wide at its base as the opening of the cavum internasale. Other specimens of *Holoptychius* show clearly that the tusks of the upper and lower jaws are about the same size. The conditions in *Holoptychius* thus seem definitely to indicate that the cavum internasale in *Porolepiformes* cannot possibly have been developed for the foremost tusk of the lower jaw but that it must have had some other function As will be shown below (p. 400) it is very likely that it housed a gland corresponding to the intermaxillary gland of the Urodeles.

The nasal cavity (*cav. nc*, figs. 38 A, 39, 42, 43, 46 A; pl. 1, figs. 1, 2; pl. 3, fig. 3; pl. 6, fig. 3) is somewhat different in shape and extent in the various *Porolepis* species. Disregarding the widened funnel-like anterior opening of the canalis olfactorius, it is in *P. spitsbergensis* almost round in dorsal and ventral aspects, but low and practically oval in lateral aspect. On the other hand, in *P. brevis* and *P. elongata* it is more extended in an antero-medial direction, stretching forwards and medially above the antero-lateral part of the cavum internasale, which in these forms is considerably shallower than in *P. spitsbergensis.* The subsequent description of the nasal cavity is based mainly on *P. spitsbergensis.*

The walls of the nasal cavity are unusually complete. On the whole they are thin and all of them are concave on the sides facing the nasal cavity.

The medial nasal wall (*w. mn*, figs. 36 A, 37 A, 39, 43; pl. 1, figs. 1, 2; pl. 2, fig. 3; pl. 5, fig. 2) is made up of the lateral part of the internasal wall which lies laterally to the cavum internasale and to the foremost portion of the ethmoidal part of the cranial cavity. Its anterior and by far longer part, which separates the nasal cavity and the cavum internasale, is thin and has such a position that its lateral side facing the nasal cavity is as a whole directed laterally and somewhat postero-dorsally. The posterior part of the wall is thick. It is situated between the nasal cavity and the foremost portion of the ethmoidal part of the cranial cavity and in *P. spitsbergensis* it participates in the posterior boundary of the cavum internasale.

The posterior nasal wall or postnasal wall (*w. pn*, figs. 36, 37 A, B, 39 B, 40 A, 43; pl. 1, figs. 3, 4; pl. 2, fig. 2; pl. 3, fig. 1) is not transverse in position but extends from behind and medially in a direction laterally and anteriorly. The lateral part of this wall is thin, but it increases gradually in thickness in a medial direction. As has already been said above in the description of its posterior face, it is pierced by several canals (*c. prm*, c_1prl, c_2prl, c_por, *c. vl*; see pp. 373—376) and partly also by the fenestra ventro-lateralis (pp. 370—371).

The lateral nasal wall (*w. al*, figs. 39, 40 A, C, 43, 46 A; pl. 3, fig. 3; pl. 6, fig. 3) has a very oblique position and its external face is directed antero-dorso-laterally. This wall is fairly thin throughout its extent. It is perforated by the fenestra endonarina anterior and by the dorso-lateral division of the fenestra ventro-lateralis which represents the fenestra endonarina posterior. The posterior part of the wall, which meets the solum nasi at a fairly pronounced angle, bears a low longitudinal crest on its medial side. This crest, the crista rostro-caudalis (*ri. w. al*, figs. 36 B, 37 B, 39, 40 A, C, 46 A; pl. 1, fig. 3; pl. 2, figs. 2, 3; pl. 3, figs. 2, 3; pl. 5, fig. 1; pl. 6, fig. 3), projects into the nasal cavity in a medial and somewhat ventral direction. It is most strongly developed at its posterior end at the border of the fenestra ventrolateralis, whence it decreases gradually forwards and disappears entirely ventrally to the posterior border of the fenestra endonarina anterior. By means of this crest, which throughout its extent is parallel with the solum nasi, the nasal cavity is imperfectly subdivided into a principal chamber and a postero-ventro-lateral recess, the lateral recess (*re. l*, figs. 36 B, 37 B, 39, 40 A, C, 42 A—C, 46 A; pl. 2, fig. 2; pl. 3, figs. 2, 3). The lateral recess as thus defined is long and low and is bounded dorsally by the crista rostro-caudalis, dorso-laterally and laterally by the postero-ventral part of the lateral nasal wall, and ventrally by the postero-lateral part of the solum nasi. Anteriorly and medially it is in open communication with the principal chamber and posteriorly it leads to the mouth cavity through the fenestra ventro-lateralis. Immediately dorsally to the crista rostro-caudalis (*ri. w. al*) is a groove running rostro-caudally on the medial side of the lateral nasal wall. This rostro-caudal groove (*gr. ntp*, figs. 39, 42 A—C, 46 A; pl. 2, fig. 2; pl. 3, figs. 2, 3; pl. 6, fig. 3) begins anteriorly a little behind the fenestra endonarina anterior and goes backwards to the division of the fenestra ventrolateralis that represents the fenestra endonarina posterior. It is shallow most anteriorly, but increases gradually in depth backwards. From its position and course it is obvious that it must have been caused by the posterior nasal tube which passed backwards in it to the dorso-lateral division of the fenestra ventro-lateralis.

The anterior nasal wall or prenasal wall (figs. 39 A, 43, 46 A; pl. 1, figs. 1, 2; pl. 6, fig. 3) is formed by the lateral part of the divisio prenasalis communis (*w. pren*). It is thin laterally at its transition into the lateral wall, but increases rapidly in thickness medially. Its posterior side facing the nasal cavity is quite smooth (cf. *Eusthenopteron*, pp. 443—445; figs. 52 A, B, 70 A, 71 A, 72 A). It is pierced by the posterior opening of the canal $c_a or$ (p. 369) and the small orifices of certain other canals (*c. prt*; pp. 373, 375).

The roof of the nasal cavity, the tectum nasi (*te. n*, figs. 39, 46 A; pl. 1, figs. 1, 2), is thin laterally at its transition into the lateral and posterior nasal walls, but it increases in thickness medially towards the medial nasal wall. As the adjacent parts of the medial and anterior walls, it is pierced by a number of canals (*c. prt*) all of which will be treated below (pp. 373—375).

The floor of the nasal cavity, the solum nasi (*sol. n*, figs. 36 A, 39, 40 A, D, 46 A; pl. 2, figs. 2, 3; pl. 3, figs. 2, 3; pl. 6, fig. 3), is fairly thin. The larger part (*ar. Vo*) of its ventral side is covered by the vomer. Its dorsal side facing the nasal cavity is only slightly concave. The postero-lateral corner of the floor is at the transition to the postnasal wall perforated by the ventro-medial division of the fenestra ventro-lateralis that represents the fenestra endochoanalis. The postero-lateral part of the floor that forms the ventral boundary of the lateral recess (*re. l*) of the nasal cavity is produced backwards into a small obtuse process (*pr. S*, figs. 36 A, 37 A, B, 40 A, C, D, 46 A; pl. 1, figs. 3, 4; pl. 2, figs. 2, 3; pl. 3, fig. 2; pl. 5, fig. 1) ventrally to the lateral portion of the endochoanal division of the fenestra ventro-lateralis. This process obviously represents Seydel's palatal process of the Urodeles and will therefore be referred to as Seydel's palatal process. It is bounded off laterally from the postero-ventral corner of the lateral nasal wall by a shallow notch, the incisura ectochoanalis (*i. ech*, fig. 40 A, D). As has already been mentioned in the description of the ventral face of the ethmoidal region (p. 359), the posterior part of the solum nasi is pierced by a canal ($c_{p}or$) which goes forwards from the orbit to the nasal cavity. The anterior opening of this canal is well exposed in one of the specimens (pl. 6, fig. 3). The canal is continued forwards across the dorsal face of the floor by a distinct groove ($gr_{a}or$, figs. 39 A, 42 B, E; pl. 6, fig. 3) leading to another canal ($c_{a}or$, figs. 39 A, 42 A—D, 43; pl. 1, figs. 1, 2; pl. 3, fig. 2; pl. 6, fig. 3) which pierces the ventro-lateral part of the prenasal wall. This groove ($gr_{a}or$) and the two canals ($c_{a}or$, $c_{p}or$) connected by it together with the groove $gr_{p}or$, (see p. 359) form the orbitorostral passage already referred to above.

The fenestra endonarina anterior (*fe. ena*, figs. 39 A, 40 A, C, 43, 46 A; pl. 2, figs. 1, 2; pl. 3, fig. 3; pl. 6, fig. 3) is situated in the anterior dorso-medial part of the lateral nasal wall. It is relatively small, oval in outline and its shape and size are exactly similar to those of the fenestra exonarina anterior (*fe. exa*, figs. 37 C, 40 B, 41, 42 A, C; pl. 1, fig. 3; pl. 2, fig. 1; pl. 3, fig. 3; pl. 4, fig. 2) which lies straight externally to it in the antero-lateral part of the ethmoidal shield. The medial side of the lateral nasal wall is quite smooth below the fenestra endonarina. The dermal bones bounding the fenestra exonarina anterior are also completely devoid of processes extending into the nasal cavity (cf. *Eusthenopteron*, fig. 52). The fenestrae endonarina and exonarina form together a short canal (*c. nta*, fig. 42 C) for the anterior external nasal tube (*nta*, fig. 43). Both the postero-ventral and antero-dorsal wall of this canal have small pocket-like recesses

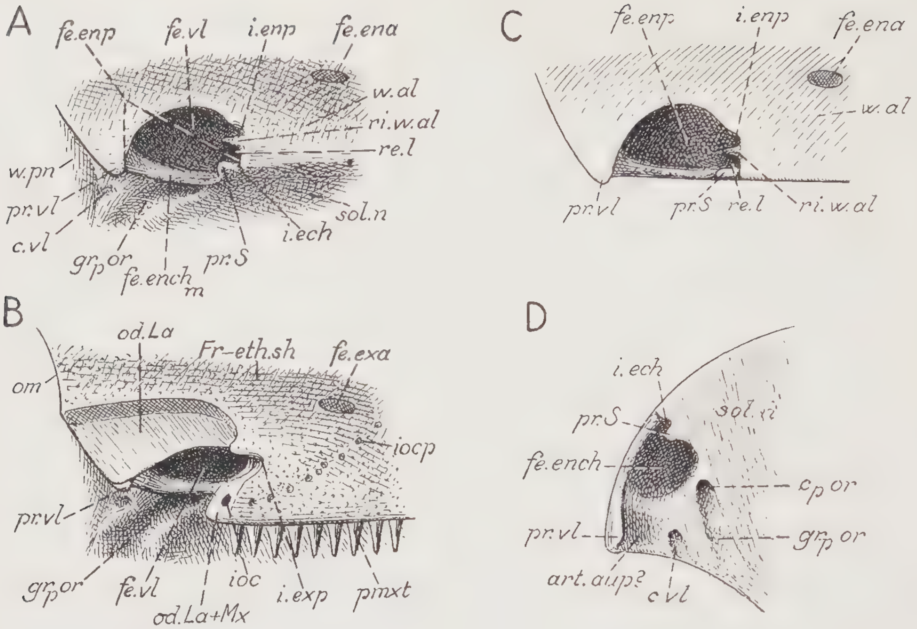

Fig. 40. *Porolepis brevis* Jarvik. *A.* Right ventro-lateral corner of the ethmoidal region in lateral and somewhat postero-ventral aspect. *B.* Same part of the ethmoidal region as in *A*, but with the dermal bones of the ethmoidal shield in position. *C, D,* same part as in *A* in lateral and ventral aspects. Restorations made after several specimens. $^6/_1$.

Fr-eth. sh, fronto-ethmoidal shield; *art. aup?,* area against which pars autopalatina probably abutted; c_p*or,* posterior canal of orbitorostral passage; *c. vl,* canal piercing the ventro-lateral part of postnasal wall; *fe. ena,* fenestra endonarina anterior; *fe. ench,* ventro-medial division of fenestra ventro-lateralis, representing fenestra endochoanalis; *fe.* $ench_m$, medial margin of ditto; *fe. enp,* dorso-lateral division of fenestra ventro-lateralis, representing fenestra endonarina posterior; *fe. exa,* fenestra exonarina anterior; *fe. vl,* fenestra ventro-lateralis; gr_p*or,* posterior groove of orbitorostral passage; *i. ech,* incisura ectochoanalis; *i. enp,* notch in the margin of fenestra ventro-lateralis for posterior nasal tube; *i. exp,* notch in the margin of ethmoidal shield for posterior nasal tube; *ioc,* infraorbital sensory canal; *iocp,* pores of infraorbital canal; *om,* margin of orbital opening; *od. La,* area of ethmoidal shield overlapped by lachrymal; *od. La + Mx,* area of ethmoidal shield overlapped by lachrymal and maxillary; *pmxt,* premaxillary tooth; *pr. S,* Seydel's palatal process; *pr. vl,* ventro-lateral process of postnasal wall; *re. l,* lateral recess of nasal cavity; *ri. w. al,* crista rostro-caudalis; *sol. n,* solum nasi; *w. al,* (antero-)lateral nasal wall; *w. pn,* postnasal wall.

(*re. nta,* fig. 42 A). What their function was is difficult to say with any certainty. They may have been occupied by bulges of the external nasal tube, but it is also possible that they served as places of origin of nasal muscles.

The fenestra ventro-lateralis (*fe. vl,* figs. 36, 37 A, B, 39 B, 40, 42 B, E, 46 A; pl. 1, figs. 3, 4; pl. 2, figs. 2, 3; pl. 3, figs. 1, 2; pls. 4, 5) which has been repeatedly referred to above is, as we have seen, an opening in the ventro-lateral corner of the ethmoidal region, bounded by the postero-lateral part of the solum nasi and adjacent parts of the postnasal wall and lateral nasal wall. As has also been pointed out this opening consists of two divisions, a dorsal lateral one which is the fenestra endonarina posterior and a ventral medial one which is the fenestra endochoanalis. The fenestra endonarina posterior (*fe. enp*, figs. 39 B, 40 A, C, 42 B, C, E) is situated in the lateral nasal wall and forms a rounded emargination in the hindmost ventro-lateral part of that wall. It is bounded posteriorly by the processus ventrolateralis (*pr. vl*) of the postnasal wall. In its anterior part there is a small but very pronounced notch (*i. enp*, figs. 36 B, 37 B, 40 A, C, 46 A; pl. 2, fig. 2; cf. fig. 43) at the posterior end of the groove (*gr. ntp*) for the posterior external nasal tube on the medial face of the lateral nasal wall. This notch must therefore have transmitted the posterior external nasal tube (*ntp*, fig. 43). Immediately ventrally to it we find the posterior end of the crista rostro-caudalis (*ri. w. al*). Ventrally to this crest opens the lateral recess (*re. l*) of the nasal cavity. The fenestra endochoanalis (*fe. ench*, figs. 36 A, 39 B, 40 D, 42 B, E, 46 A) is in ventral view fairly oval in outline. It consists of two parts, one directed ventrally (*fe. ench*, fig. 42 B) and lying in the solum nasi, and one directed posteriorly (*fe. ench*, figs. 39 B, 42 E) and forming an emargination in the ventro-lateral part of the postnasal wall immediately medially to the processus ventro-lateralis.

As shown in fig. 40 the dorsal part of the fenestra endonarina posterior is covered by the postero-ventro-lateral part of the ethmoidal shield. On the outside of this part of the ethmoidal shield there is a depressed unornamented area (*od. La*, figs. 37, 40 B) which must have been overlapped by the lachrymal. Antero-ventrally to this overlapped area the part of the ethmoidal shield formed by the lateral rostral and premaxillary projects backwards as a process, on the outside of which another unornamented area (*od. La* + *Mx*, figs. 37 B, C, 40 B; pl. 2, fig. 1; pl. 3, fig. 2; pl. 4, fig. 2; pl. 5; cf. fig. 46 A) is developed. On the latter area we find the posterior opening of the part of the infraorbital sensory canal that is enclosed in the lateral rostral (*ioc*, figs. 36 A, 37, 40 B; pl. 3, fig. 1; pl. 4) and it is therefore quite obvious that this area too was overlapped by the lachrymal, more precisely by the antero-ventral corner of that bone. However, it is likely that the lachrymal was not attached to the lowermost part of this area, but that this was overlapped by the maxillary. Between the two overlapped areas (*od. La*, *od. La* + *Mx*) just dealt with is a distinct notch, *i. exp* (figs. 36, 37, 40 B, 46 A; pl. 1; fig. 3; pls. 2, 4; pl. 5, fig. 2; cf. fig. 41), which lies just laterally to the similar notch (*i. enp*) for the posterior external nasal tube in the anterior margin of the fenestra endonarina posterior. When the dermal bones of the cheek are in their natural position, the notch *i. exp* is closed from behind by the lachrymal so as to form the fenestra exonarina posterior (*fe. exp*, fig. 41). The shape of the anterior end of the lachrymal just behind the fenestra exonarina posterior could not be decided, but since in the closely related genus *Holoptychius* (fig. 33) it is clearly notched at this very place it probably was so also in *Porolepis*.

The dermal bones of the palate are still imperfectly known and the boundaries of the fenestra exochoanalis in *Porolepis* (*fe. exch*, fig. 46 A) are therefore not fully clear. It is conceivable, however, that this fenestra was fundamentally as the corresponding one in *Eusthenopteron* (*fe. exch*, figs. 56, 87 A). We may thus assume that it was bounded laterally by the premaxillary and the maxillary, postero-medially by the dermopalatine and antero-medially by the vomer.

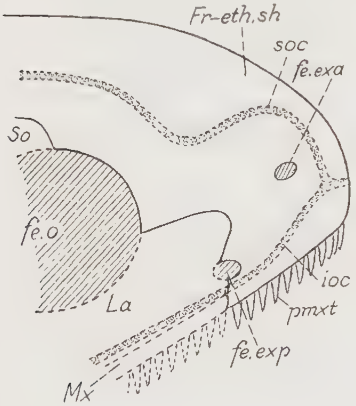

Fig. 41. *Porolepis brevis* Jarvik. Restoration of the lateral aspect of the anterior parts of the fronto-ethmoidal shield and cheek. $^{3}/_{1}$.

Fr-eth. sh, fronto-ethmoidal shield; *La*, lachrymal; *Mx*, maxillary; *So*, supraorbital; *fe. exa*, fenestra exonarina anterior; *fe.exp*, fenestra exonarina posterior; *fe. o*, orbital opening; *ioc*, infraorbital sensory canal; *pmxt*, premaxillary tooth; *soc*, supraorbital sensory canal.

Of the various canals in the anterior parts of the endocranium the canalis olfactorius has already been treated. The other canals are, as we have seen from the description of their orifices, of widely different calibres. The finer ones are variable both as regards position and number, and frequently not only in different specimens of the various species, but also on the right and left sides in one and the same specimen. The subsequent account refers mainly to the conditions in *P. spitsbergensis*.

On the lower side of the tectum orbitale (*te. o*), laterally and posteriorly to the posterior orifice of the medial profundus canal, we find two fairly small foramina which are connected by a groove. These foramina are the ventral orifices of two canals (*c. prdl*, figs. 36 A, 43; pl. 1, figs. 1, 4; pl. 2, figs. 2, 3) which pass upwards and forwards and presumably transmitted branches from the n. profundus given off in the orbit. Judging from the course of the canals these profundus branches seem to have been distributed to parts of the skull-roof and skin situated behind the fenestra exonarina anterior. Postero-medially to the posterior orifice of the medial profundus canal there is still another small foramen, which forms the ventral orifice of the canal *c. prd* (fig. 36 B; pl. 1, figs. 1, 3, 4; pl. 2, fig. 3) described above (p. 362). This fine canal, which ascends to the pit in which lies the posterior orifice of the canal for the r. ophthalmicus lateralis, may have been traversed by a dorsal profundus branch.

The canal for the r. ophthalmicus lateralis (*c. o. lat*, figs. 36 B, 37 B; pl. 1, figs. 3, 4; pl. 3, fig. 1; pl. 4, fig. 1; pl. 5, fig. 1) has its posterior orifice, as we already have seen, in the foremost dorsal part of the orbitotemporal region from where it pierces the thick dorso-medial part of the postnasal wall. However, it could be traced only a short distance forwards. In the fracture sections through the anterior parts of the snout in which are seen the supraorbital sensory canal and adjacent parts of the endocranium no signs of it were found. Very likely it soon led up to the dorsal face of the ethmoidal region, so that in the anterior parts of the snout the r. ophthalmicus lateralis ran between the endocranium and the ethmoidal shield as in *Eusthenopteron* (cf. p. 471). That the r. ophthalmicus did not enter the nasal cavity could be established with certainty.

In the ventral part of the deep pit housing the posterior orifice of the canal for the r. ophthalmicus lateralis lies the dorsal orifice of the canal *c. prd* described above. Laterally to this the pit also contains the ventral orifices of two somewhat wider canals (*c. vadl*, figs. 36 B, 43; pl. 1, fig. 4) which go upwards and a little forwards through the tectum orbitale. Both these canals open on the dorsal side of the foremost part of the tectum orbitale medially to the dorsal orifices of the canals *c. prdl*. Their position and course thus indicate that they may very well have given passage to twigs of the presumed profundus branch ascending through the canal *c. prd*. However, as each of them is wider than the canal *c. prd*, it is conceivable that they were mainly developed for vessels. The possibility must also be taken into account that one or both of them may have been traversed also by twigs of a profundus branch accompanying the r. ophthalmicus lateralis.

The medial profundus canal (*c. prm*, figs. 36 B, 37 B, 38 A, 39 B, 42; pl. 1; pl. 2, fig. 2; pl. 3, fig. 1; pl. 5, fig. 1; cf. fig. 43) pierces the postnasal wall. This canal is short and very wide, wider even than the canalis olfactorius. It goes forwards and a little medially, opening anteriorly into the nasal cavity immediately dorso-laterally to the anterior opening of the canalis olfactorius. From its dorso-medial side issue two fairly fine canals, one anterior (*$c_1$prdm*) and one posterior (*$c_2$prdm*), which both ascend medially and somewhat anteriorly through the postnasal wall (fig. 42 A, D; pl. 1, figs. 1, 2; pl. 2, fig. 3) and presumably gave passage to dorso-medial profundus branches. The medial part of the tectum nasi and the adjacent dorsal parts of the medial and anterior nasal

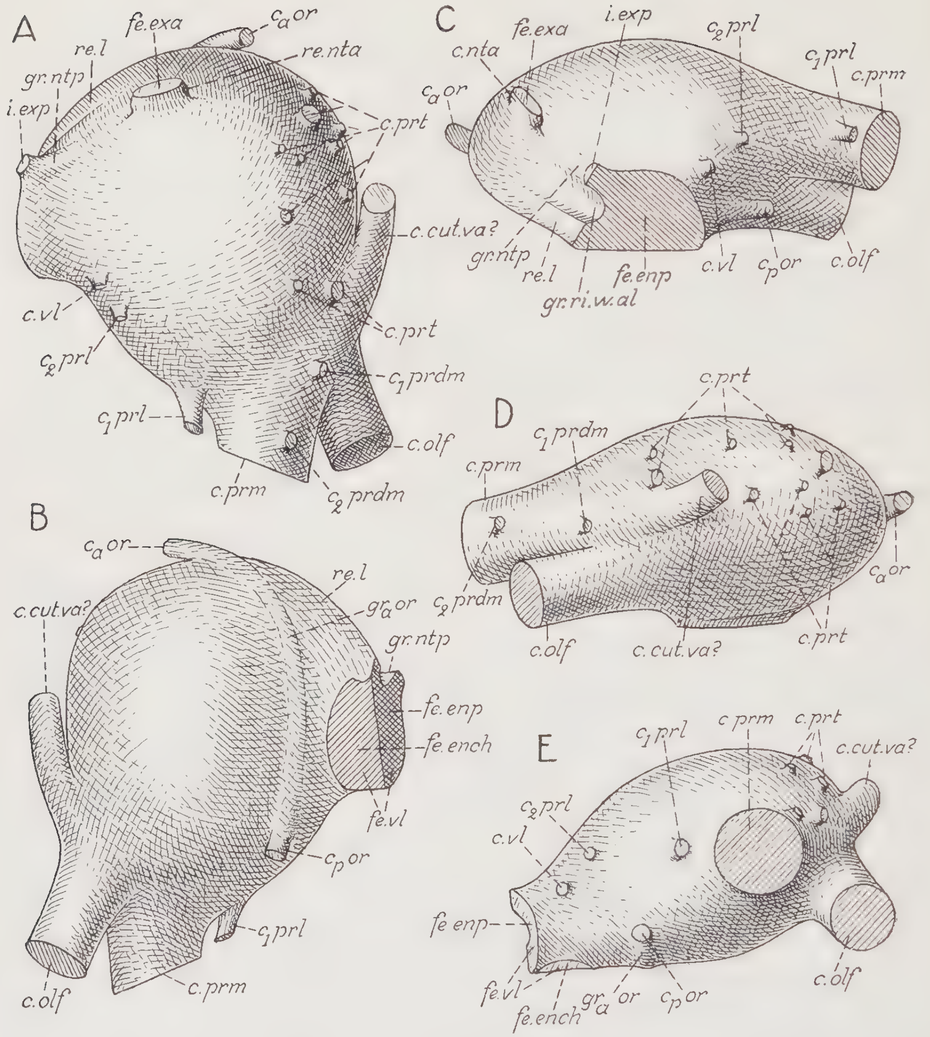
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Fig. 42. *Porolepis spitsbergensis* Jarvik. Restoration of the cast of the left nasal cavity, *A*, dorsal, *B*, ventral, *C*, lateral, *D*, medial, and *E*, posterior aspect. Certain details after *P. brevis*. $^3/_1$.

c_a*or*, anterior canal of orbitorostral passage; *c. cut. va?*, canal, probably for profundus branch but possibly also for cutaneous vessel; *c. nta*, canal for anterior nasal tube; *c. olf*, canalis olfactorius; c_p*or*, posterior canal of orbitorostral passage; *c. prm*, medial profundus canal; *c. prt*, canal for twig of medial terminal profundus branch; *c. vl*, canal piercing the vento-lateral part of postnasal wall; c_1*prdm*, c_2*prdm*, canals for dorso-medial profundus branches; c_1*prl*, c_2*prl*, lateral profundus canals; *fe. ench*, division of fenestra ventro-lateralis representing fenestra endochoanalis; *fe. enp*, division of fenestra ventro-lateralis representing fenestra endonarina posterior; *fe. exa*, fenestra exonarina anterior; *fe. vl*, fenestra ventro-lateralis; gr_a*or*, anterior groove of orbitorostral passage; *gr. ntp*, groove for posterior nasal tube; *gr. ri. w. al*, groove for crista rostro-caudalis; *i. exp*, notch in the margin of the ethmoidal shield for posterior nasal tube; *re. l*, lateral recess of nasal cavity; *re. nta*, recess in the wall of canal for anterior nasal tube, possibly for nasal muscles.

walls are pierced, in front of the medial profundus canal, by ten fairly short canals of different calibres (*c. prt*, figs. 39 A, 42 A, D, E, 43, 46 A; pl. 1, figs. 1, 2; pl. 2, fig. 3) which all ascend from the nasal cavity to the dorsal face of the ethmoidal region. Judging from their position these canals gave exit to dorsal twigs of the medial terminal profundus branch and were probably traversed also by vessels. Certain of them may perhaps have given passage to vessels only. Another canal (*c. cut. va*?, figs. 39 B, 42 A, B, D, E, 43; pl. 1, figs. 1, 2) leaving the nasal cavity is much wider than those just described and goes from the postero-medial corner of the nasal cavity forwards and dorso-medially in a direction towards the dorsal part of the cavum internasale. Its posterior orifice lies in the postero-medial corner of the nasal cavity in the medial nasal wall and close in front of the anterior orifices of the canalis olfactorius and medial profundus canal. Its relations to the last-mentioned canals are such that it probably transmitted a strong branch of the n. profundus and also a vessel which further posteriorly accompanied the n. olfactorius. This vessel may have given off or, if a vein, received branches from the dorso-medial parts of the ethmoidal region (cf. *Eusthenopteron*, pp. 469—470; *c. cut. va*, fig. 57).

The lateral profundus canal ($c_1 prl$, figs. 36 B, 37 B, 39 B, 42 A, B, C, E; pl. 1, figs. 3, 4; pl. 2, fig. 2; pl. 3, fig. 1; pl. 5, fig. 1; pl. 6, fig. 3; cf. also fig. 43) which is fairly narrow and which presumably gave passage to a lateral profundus branch issuing from the n. profundus while still in the orbit, pierces the postnasal wall a little laterally to the medial profundus canal and goes forwards to the dorsal part of the nasal cavity. Laterally to this canal there are at least in *P. brevis* and *P. elongata* some other fine canals ($c_2 prl$, figs. 37 B, 39 B, 42 A, C, E; pl. 3, fig. 1; pl. 5, fig. 1), variable both as to number and position, which are also referred to here as lateral profundus canals. They go from the orbit forwards into the postnasal wall, but whether they actually open into the nasal cavity could not be established. Judging from their direction they must have been developed for nerve branches or branches of vessels coming from the medial parts of the orbit.

The hindmost part of the orbitorostral passage (p. 369) formed by the groove $gr_{p}or$ (see p. 359; figs. 37 A, B, 40; pl. 3, figs. 1, 2; pl. 4, fig. 1) has such a position and direction that it must have been developed for a branch of the n. profundus and for vessels coming from the medial parts of the orbit. A profundus branch reaching the foremost part of the snout through this passage (fig. 42 B) must have traversed the nasal cavity medially to the choana and ventrally to the lateral part of the nasal sac.

The canal *c. vl* (figs. 37 A, B, 39 B, 42 A, C, E; pl. 3, figs. 1, 2; pl. 4, fig. 1; pl. 5) seems, as far as may be judged from the position and development of its posterior orifice (p. 359), to have given passage to a fine lateral twig of the profundus branch, which ran forwards through the orbitorostral passage. As already mentioned this canal in certain cases may be subdivided into two.

Disregarding the part of the infraorbital sensory canal enclosed in the lateral rostral (*ioc*, figs. 36 A, 37, 40 B, 41, 46 A; pls. 3, 4), the part of the cranium situated laterally to the fenestra exochoanalis shows no important canals either in the endocranium itself or in the dermal bones situated outside it. I have not even found a canal for the r. buccalis lateralis. Under these conditions and since the canals (the lateral profundus canals, the orbitorostral passage, and the canal *c. vl*) passing to the lateral parts of the snout all leave the orbit in such a direction that they must have been traversed by nerves and vessels coming from the medial parts of the orbit, we are forced to the conclusion that the lateral parts of the snout were innervated mainly by lateral branches of the n. profundus. It follows also that the vascular supply of the lateral parts of the snout took place through arteries which behind the ethmoidal region ran in the medial part of the orbit.

If the above interpretations of the various canals piercing the postnasal wall in a forward direction are in the main true, the n. profundus was on the whole developed as follows in the foremost part of the orbit and in the ethmoidal region.

The n. profundus (*n. pr*, fig. 43) in *Porolepis* was a strong nerve. During its course forwards in the anterior part of the orbit it divided into the following branches: 1) A dorsal branch, *r. pras*, which accompanied the r. ophthalmicus lateralis through the canal *c. o. lat* and went to the dorso-medial parts of the snout. Twigs of this branch may have ascended through the canals *c. vadl*. 2) A lateral, fairly strong branch, *r. pror*. This branch went forwards through the orbitorostral passage, crossing the nasal cavity medially to the choana and ventrally to the lateral part of the nasal sac. It supplied the antero-ventro-lateral part of the snout. Shortly before leaving the orbit it probably gave off a branch, *r. prvl*, which went to the postero-ventro-lateral part of the nasal cavity through the canal *c. vl*. 3) One or a few lateral branches, *r. prl*, which went to an area dorsally to the postero-lateral part of the nasal sac through the canals c_1prl and c_2prl. 4) A dorso-lateral branch, *r. prdl* which below the tectum orbitale bifurcated into two main branches. These two branches (*rr. prdl*) went upwards and forwards through the canals *c. prdl*, supplying an area of the skull-roof and skin situated behind the fenestra exonarina anterior. 5) A fairly weak dorsal branch, *r. prd*, which after traversing the canal *c. prd* either continued through

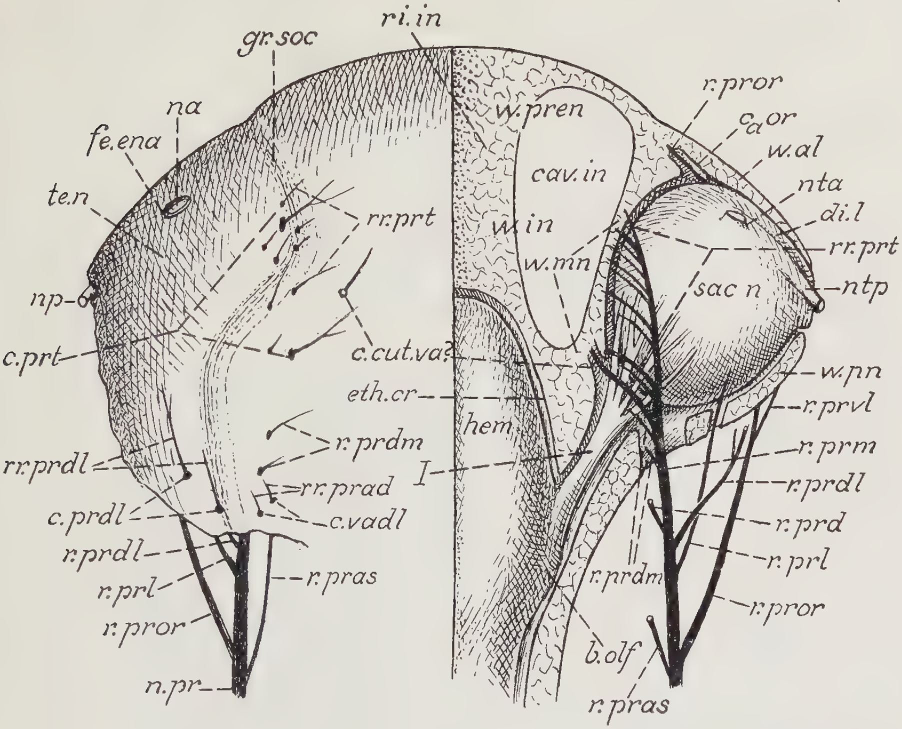

Fig. 43. *Porolepis spitsbergensis* Jarvik. Attempted restoration of the anterior part of the endocranium, the right nasal sac, the anterior part of the brain, and the n. profundus. Dorsal view. The dorsal parts of the endocranium of the right side removed. $^2/_1$. *b. olf,* bulbus olfactorius; c_a*or,* anterior canal of orbitorostral passage; *cav. in,* cavum internasale; *c. cut. va?,* canal, probably for profundus branch, but possibly also for cutaneous vessel; *c. prdl,* canal, probably for dorso-lateral profundus branch; *c. prt,* canals for twigs of medial terminal profundus branch; *c. vadl,* canals directed dorso-laterally, probably for branch of n. profundus and vessel; *di. l,* lateral diverticle of nasal sac; *eth. cr.* ethmoidal part of cranial cavity; *fe. ena,* fenestra endonarina anterior; *gr. soc,* groove for ridge on lower face of fronto-ethmoidal shield housing supraorbital sensory canal; *hem,* hemisphere of forebrain; *na, np,* anterior and posterior external nostrils; *n. pr,* n. profundus; *nta, ntp,* anterior and posterior nasal tubes; *ri. in,* internasal ridge; *r. pras,* branch of n. profundus accompanying r. ophthalmicus lateralis; *r, prd,* dorsal branch of n. profundus; *r. prdl,* dorso-lateral profundus branch; *r. prdm,* dorso-medial branch of medial terminal profundus branch; *r. prl,* lateral terminal profundus branch; *r. prm,* medial terminal profundus branch; *r. pror* orbitorostral terminal profundus branch passing through orbitorostral passage; *r. prvl,* branch of orbitorostral terminal profundus branch passing through the canal *c. vl*; *rr. prad,* branches of *r. pras* or *r. prd* of n. profundus; *rr. prdl,* branches of *r. prdl,* of n. profundus; *rr. prt,* twigs of medial terminal profundus branch; *sac n,* nasal sac; *te. n,* tectum nasi; *w. al,* lateral nasal wall; *w. in,* internasal wall; *w. mn,* medial nasal wall; *w. pn,* postnasal wall; *w. pren,* divisio prenasalis communis; *I,* n. olfactorius.

one of the canals *c. vadl* or accompanied the branch *r. pras* through the canal *c. o. lat.* 6) A very strong medial branch, *r. prm,* which through the medial profundus canal (*c. prm*) went to the nasal cavity. This branch, the medial terminal profundus branch, which formed the remainder of the profundus nerve after the giving off of all the other branches mentioned, sent out two dorso-medial branches, *r. prdm*, passing through the canals c_1prdm and c_2prdm in the postnasal wall. Within the nasal cavity it ran forwards dorsally to both the n. olfactorius (*I*) and the postero-medial part of the nasal sac (*sac n*). In the posterior part of the nasal cavity it gave off a strong dorso-medial branch through the canal *c. cut. va*?, then breaking up into numerous small branches or twigs (*rr. prt*), many of which went upwards through the canals *c. prt* to innervate the skull roof and the skin on the dorso-medial parts of the snout.

Regarding the other nerves of the snout the conditions seem on the whole to have been as follows.

As there are no important canals for vessels and nerves in the postero-ventro-lateral part of the snout and since the lateral parts of the snout, as has been shown, must in all probability have been supplied by the n. profundus, it is obvious that the r. maxillaris must have been weakly developed. It is even possible that this nerve did not extend forwards beyond the orbit, but ended somewhere at the most anterior part of the palatoquadrate.[1]

The r. ophthalmicus lateralis, probably accompanied by profundus branches and vessels, must have left the orbit through the canal *c. o. lat*, through which it reached the dorsal face of the ethmoidal region. On this face it may have continued forwards in the groove *gr. soc*, between the endocranium and the dermal bones (cf. fig. 59).

Nothing certain is known so far concerning the course of the r. buccalis lateralis. It is not impossible, however, that branches of this nerve may have accompanied the profundus branch *r. pror* through the orbitorostral passage (cf. p. 394).

Finally it may be mentioned that the r. palatinus VII seems to have pierced the vomer in a short and rather wide rostro-caudal canal. In the single specimen in which it is known this canal (*c. pal*, fig. 37 A, pl. 5, fig. 2) is situated in the postero-medial part of the vomer. Otherwise nothing can be made out concerning the course of the r. palatinus VII.

Regarding the course of the vessels it may be particularly pointed out that the lateral parts of the snout presumably both received their blood and were drained by vessels which behind the ethmoidal region passed through the medial part of the orbit. There existed no large arteries and veins passing through the postero-ventro-lateral part of the snout. On the whole the vessels of the snout accompanied the nerves and their course and distribution were therefore somewhat similar. No canal that may have transmitted a v. cerebralis anterior has been found and thus nothing can be said concerning this vein.

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[1] Small branches may have been overlooked or may have traversed the orbitorostral passage.

b. Genus Holoptychius Agassiz.

(Figs. 33, 44).

Previous investigations. — Owing to its poor state of preservation in the material previously available the snout in *Holoptychius* has been very unsatisfactorily known hitherto (Woodward 1891; Traquair 1895; Goodrich 1909, pp. 280—285, figs. 251, 254 A; Watson and Day 1916, pp. 2—7, fig. 1; Holmgren and Stensiö 1936, pp. 344—363, fig. 274; Westoll 1937, fig. 1 C; 1937 a, fig. 9 c; Moy-Thomas 1939 a, fig. 19 B). Its endocranial parts, the palatoquadrate, and the dermal bones of the palate were completely unknown. The position of the external nasal apertures could not be established. Our knowledge of the snout in *Holoptychius* has so far been confined to the general development of the hinder postrostral and nasal bones.

Material. — The material of *Holoptychius* to be dealt with here includes a few specimens from the uppermost Upper Devonian of East Greenland and some specimens of *H. flemingi* Agassiz.

The Greenland specimens were collected during Dr. Lauge Koch's expeditions in 1932 (G. G. U. No. 478; cf. Säve-Söderbergh 1933) and 1934 (G. G. U. Nos. 494, 495, 496; cf. Johansson 1935) and belong to the Zoological Museum of the University of Copenhagen. One of these specimens (fig. 44) is a large part of the divisio cranialis anterior and is as a whole fairly well preserved. It is, however, deficient on the left side, where inter alia the nasal capsule is missing. The right nasal capsule is badly crushed. The restoration shown in fig. 33 is based on the other Greenland specimens, mainly on a single specimen (G. G. U. No. 496), in which the dermal bones bounding the fenestra exonarina communis are well preserved.[1]

The specimens of *H. flemingi* here examined, which belong to the Sedgwick Museum of Geology, Cambridge, and the Swedish Museum of Natural History in Stockholm, show the general disposition of the dermal bones of the skull-roof and cheek and the general course of the sensory

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[1] The Greenland specimens in question were found in deposits in which typical *Holoptychius* scales are abundant (Stensiö 1931, pp. 198—200). As far as they can be compared to *H. flemingi* (Woodward 1891, fig. 49; Goodrich 1909, fig. 251; Watson and Day 1916, fig. 1; Holmgren and Stensiö 1936, fig. 274; Westoll 1937, fig. 1 C; 1937 a, fig. 9 c), the pattern of the dermal bones is fundamentally as in that species. Everything thus seems to show that they must belong to the genus *Holoptychius*. Since they cannot be placed with certainty to any of the previously known *Holoptychius* species, they will preliminarily be referred to as *Holoptychius* sp.

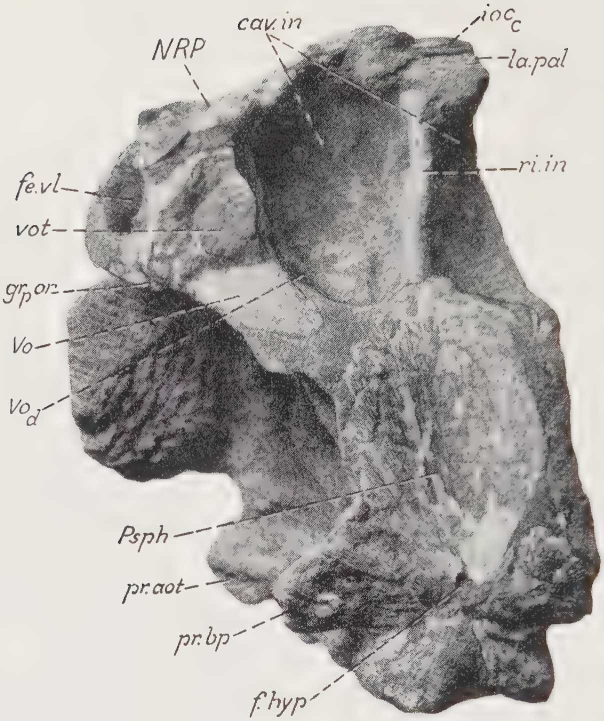

Fig. 44. *Holoptychius* sp. Ventral aspect of an imperfect divisio cranialis anterior. Upper Devonian (Remigolepis Series) of the N. slope of Mt. Celsius (the Western Upper Terrace), East Greenland. Specimen G. G. U. No. 478, belonging to the Zoological Museum of the University of Copenhagen. $^2/_1$.

NRP, "premaxillary" (rostro-premaxillary or naso-rostro-premaxillary); *Psph*, parasphenoid; *Vo*, vomer; *Vo_d*, ascending lamina of vomer; *cav. in*, cavum internasale; *fe. vl*, fenestra ventro-lateralis of nasal capsule; *f. hyp*, foramen in parasphenoid for ventral division of fossa hypophyseos; *$gr_p or$*, posterior groove of orbitorostral passage; *ioc_c*, ethmoidal commissural canal of infraorbital sensory canals; *la. pal*, palatal lamina of ethmoidal shield; *pr. aot*, antotic process; *pr. bp*, basipterygoid process; *ri. in*, internasal ridge; *vot* vomerine tusk.

canals quite distinctly. In addition it is also seen in them that there is a fenestra exonarina communis (see pp. 381—382), situated as in the Greenland species. On the other hand nothing is seen of the endocranium and palate.

Description. — An exhaustive account of the structure of the snout will not be given here. Only such details will be entered upon as are of importance for a comparison with *Porolepis*.

In the *Holoptychius* specimen from East Greenland displaying the divisio cranialis anterior (fig. 44) we find, on the ventral side of the ethmosphenoid, a broad parasphenoid (*Psph*) and in front of this, on the lower side of the ethmoidal region, a paired deep cavum internasale (*cav. in*) separated from the corresponding cavity of the other side by an internasal ridge (*ri. in*), as in *Porolepis* (cf. figs. 36 A, 37 A). However, the cavum internasale is much deeper and wider and the internasal ridge much narrower than in any of the *Porolepis* species.

The fact that the internasal ridge is high and very narrow posteriorly proves that the cranial cavity can have extended but slightly forwards into the ethmoidal region. The ethmoidal part of the cranial cavity was therefore certainly shorter than in *Porolepis* The vomer (*Vo*) has a position corresponding to that in *Porolepis.* It is of interest to note that the vomer here is provided with an antero-medial ascending lamina (Vo_d) lining the lateral wall of the cavum internasale of its side. The base of a large tusk (*vot*) is preserved on the vomer, and it is clearly seen that the diameter of this tusk is very small compared with the width and length of the cavum internasale. Though the postero-lateral part of the ventral face of the ethmoidal region is somewhat damaged, it nevertheless shows a small triangular depressed area similar to the one in *Porolepis* (p. 359). The details of this triangular area are also much as in *Porolepis.* It thus presents a groove (gr_por) and immediately in front of this a canal (c_por, not shown in fig. 44) which represent the similarly situated formations in *Porolepis* (figs. 37 A, 40 D). A canal corresponding to the canal *c. vl* in *Porolepis* is also developed, though not shown in fig. 44. Laterally to the depressed triangular area just described we find the fenestra ventro-lateralis (*fe. vl*) of which the division representing the fenestra endochoanalis is well preserved (cf. p. 371). The posterior face of the ethmoidal region shows a distinct olfactory ridge and at least two posterior orifices of canals equivalent in position and relative size to the posterior orifices of the medial profundus canal (cf. figs. 36 B, 37 B, *c. prm*) and the canal for the ophthalmicus lateralis (*c. o. lat*) in *Porolepis.*

In *Porolepis* there is, as we have seen, in the exoskeleton outside the nasal capsule, both a fenestra exonarina anterior (*fe. exa*, fig. 41) developed for the anterior external nasal tube, and a fenestra exonarina posterior (*fe. exp*) developed for the posterior external nasal tube. On the other hand, in *Holoptychius* there is only one such opening on either side. As is shown by fig. 33, this opening in *Holoptychius* (*fe. ex*) is bounded posteriorly by the deeply notched anterior end of the lachrymal. The fact that the lachrymal thus takes part in its boundary shows that the opening in question represents at least the fenestra exonarina posterior in *Porolepis.* However, as it is larger and goes considerably further forwards than the fenestra exonarina posterior in *Porolepis*, and since there is no independent fenestra exonarina anterior, the large opening in question in *Holoptychius* probably includes both the fenestra exonarina anterior and the fenestra exonarina posterior. It is thus conceivably a fenestra exonarina communis.

It is obvious from the above brief statements that as regards most of the essential features of its snout *Holoptychius* greatly resembles *Porolepis.* In addition it could be established by the writer, with the large material at his disposal, that *Holoptychius* and *Porolepis* also agree well in the development of the other parts of the skull. It is thus quite obvious that the two genera must be closely akin.

As will be demonstrated below (pp. 488—494, 593—597) *Porolepis* and *Holoptychius* differ from the other Crossopterygians here dealt with not only in the structure of the snout but also in certain other characters. They thus evidently represent a group of their own among the Crossopterygians, a group for which the term *Porolepiformes* has been introduced in this work.

2. **Comparative section.**

a. **Comparison with Selachians and other Elasmobranchs.**

In the account of the Selachians above (pp. 250—256) only *Chlamydoselachus* was dealt with in any detail. *Porolepis* will therefore now be compared first of all with that form.

Porolepis and *Chlamydoselachus* (figs. 2—4) agree in certain of the general characters of the ethmoidal region. The nasal cavity is thus in both forms situated in the lateral portion of the ethmoidal region, the two cavities being far apart. Its walls are very complete, and even a complete medial wall is present. The internasal wall is very wide, whereas the divisio prenasalis communis is short. The cavum precerebrale (p. 251, *cav. prec*) in sharks, which in embryonic stages houses the foremost portion of the brain (ALLIS 1923, p. 130) and in adults communicates with the cranial cavity through a wide opening, the fenestra precerebralis, represents simply the ethmoidal part of the cranial cavity. If the thin roof of the ethmoidal part of the cranial cavity disappeared (cf. figs. 3 and 43), a corresponding cavity would arise also in *Porolepis.* It is also easily seen that the cavum internasale in *Porolepis* corresponds in position to the unpaired median subethmoidal depression in *Chlamydoselachus* which lies ventrally to the cavum precerebrale and is separated from this by the internasal lamina (*la. in*). If the internasal ridge (*ri. in*, figs. 36 A, 37 A) between the cavi internasales in *Porolepis* is removed, there arises a large unpaired median cavity which in all respects agrees with the subethmoidal depression in *Chlamydoselachus.* In this connection it is interesting to note that in several other sharks, e. g. *Squalus*, the subethmoidal depression is divided into right and left halves by a rostro-caudal keel or ridge which is suggestive of the internasal ridge in *Porolepis.* In certain sharks, such as *Heptanchus* (Holmgren 1941, p. 4), this keel is present in embryos, whereas it is absent in the adults.

In both *Porolepis* and *Chlamydoselachus* the divisio prenasalis communis forms a broad short rostral process which lies dorsally to the foremost parts of the infraorbital sensory canals and is a dorsal rostral process. The rostral process in both forms is bounded off laterally on either side by a notch from the lateral part of the divisio which constitutes the prenasal wall. In *Porolepis* this notch is occupied by a ridge on the lower side of the ethmoidal shield (cf. fig. 1, *ri. soc*), which houses the foremost part of the supraorbital sensory canal; in *Chlamydoselachus*, on the other hand, it is occupied by the foremost end, which bends upwards, of the infraorbital sensory canal.

In *Chlamydoselachus* (figs. 2—4) the fenestra endonarina anterior and posterior are both situated in the antero-ventral part of the lateral nasal wall. They lie close to each other and are separated by an independent cartilage, the ala nasalis (*al. n*). In *Porolepis* (figs. 39, 40 A, C, 46 A), on the other hand, the fenestra endonarina anterior is situated in the antero-dorsal and the fenestra endonarina posterior in the postero-ventral part of the lateral nasal wall and they are separated from each other by part of that wall. There is no equivalent to the ala nasalis.

The nasal fontanelle in *Chlamydoselachus* (*font. n*, fig. 4) is an opening in the solum nasi. It lies medially to the infraorbital sensory canal (*ioc*), which passes between it and the fenestrae endonarinae. In its position the nasal fontanelle thus agrees with the fenestra endochoanalis in *Porolepis*, other Rhipidistid Crossopterygians, and Amphibians (*fe. ench*, figs. 13 A, 16 B, 22 A, 23 B, 36 A, 40 D, 46, 48, 53). The nasal fontanelle, which besides in *Chlamydoselachus* is present in several other sharks, in rays (Holmgren 1941) and at least in certain Arthrodires (see p. 389), is according to Allis (cf. p. 252) the homologue of the fenestra endochoanalis. It is closed by a membrane, however, while the fenestra endochoanalis is developed for the internal nasal tube. As we know, there is no internal nasal tube nor internal nasal opening (choana) in *Chlamydoselachus* and other recent Elasmobranchs and there is no evidence whatever in the embryonic development of the ethmoidal region and the olfactory organs to indicate that the Elasmobranchs have arisen from forms with an internal nasal opening (cf. p. 252). Nor do any forms among the fossil Elasmobranchs possess such an opening. There is thus nothing to show that the nasal fontanelle is a vestige of a primary internal nasal opening. That the nasal fontanelle was present in the ancestors of the Crossopterygians and that the development in them of an internal nasal aperture was preformed by such a fontanelle is very unlikely as the choana probably was primarily absent in *Coelacanthiformes* (cf. No. 23, p. 649).

The postnasal wall has very much the same position in *Porolepis* as in *Chlamydoselachus*. The processus ventro-lateralis in *Porolepis* (*pr. vl*, figs. 37, 40) in several respects reminds of the ectethmoid process in *Chlamydoselachus* (*pr. ece*, figs. 2—4). The processus ventro-lateralis lies immediately postero-laterally to the fenestra endochoanalis and on its medial face there is a facet (*art. aup*?) against which the palatoquadrate seems to have articulated. The ectethmoid process projects from the ethmoidal region immediately postero-laterally to the nasal fontanelle, which has a position corresponding to that of the fenestra endochoanalis. The palatoquadrate articulates against the medial side of this process.

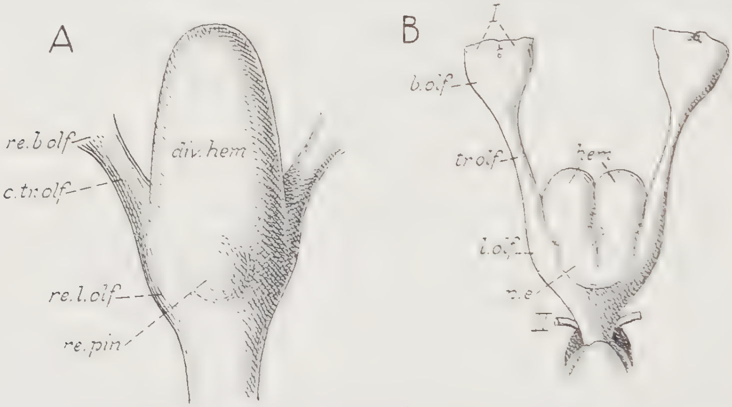

Fig. 45. *A. Porolepis spitsbergensis.* Same cast as in fig. 38 A, but interpreted as though it had housed a forebrain of Selachian type. *B. Heterodontus francisci.* Anterior part of brain in dorsal view. From DANIEL (1934, fig. 210 A).

b. olf, bulbus olfactorius; *c. tr. olf*, canal possibly for tractus olfactorius; *div. hem*, division of cranial cavity, lodging forebrain hemispheres; *hem*, hemispheres of forebrain; *l. olf*, lobus olfactorius; *p. e*, pallial eminence; *re. b. olf*, recess possibly for bulbus olfactorius; *re. l. olf*, recess possibly for lobus olfactorius; *re. pin*, recess for pineal organ and possibly also for pallial eminence; *tr. olf*, tractus olfactorius; *I*, n. olfactorius; *II*, n. opticus.

The nasal cavity is divided into a principal cavity and a lateral recess (*re. l*) in *Porolepis* (figs. 39, 42), whereas it shows no indication whatever of any subdivision into compartments in Selachians. The rostro-caudal crest (*ri. w. al*, figs. 39, 40 A, C) of the nasal cavity and Seydel's palatal process (*pr. S*, fig. 40 A, D), which are distinctly developed in *Porolepis*, are both absent in Selachians.

Judging from the shape of the foremost division of the cranial cavity and the olfactory canals, the forebrain and olfactory nerves in *Porolepis* were presumably fundamentally as in Urodeles (pp. 395—396). Comparisons with sharks show, however, that the forebrain in *Porolepis* may perhaps, though less likely, have been developed in another way.

A forebrain of a type like that of *Heterodontus* (fig. 45 B) fits also into the foremost division of the cranial cavity and olfactory canals of *Porolepis* (fig. 45 A; cf. fig. 38). It is thus obvious that the forebrain in *Porolepis* may have been shark-like. If, contrary to what may reasonably be assumed, this was so, the canalis olfactorius (*c. tr. olf*, fig. 45 A) was not developed for the olfactory nerve but for the tractus olfactorius (*tr. olf*, fig. 45 B). The bulbus olfactorius (*b. olf*) would then have lain close to the nasal sac in the widened funnel-like anterior orifice (*re. b. olf*) of the olfactory canal, whereas the lobus olfactorius (*l. olf*) would have occupied the lateral recess (*re. l. olf*) of the forebrain division of the cranial cavity. The recess for the pineal organ (*re. pin*) would in such a case have housed perhaps not only the pineal organ, but also an equivalent to the pallial eminence (*p. e*; cf. Daniel 1934, p. 232, fig. 213) in sharks.

The canal for the r. ophthalmicus lateralis (*c. o. lat*) in *Porolepis* (figs. 36 B, 37 B) seems to have been developed about as in *Chlamydoselachus* (figs. 2, 3) and thus the r. ophthalmicus lateralis in *Porolepis* probably had on the whole the same course as in *Chlamydoselachus*. The development of the other canals in the snout of *Porolepis* shows, however, that as regards its other nerves and its vessels *Porolepis* must have been very different from *Chlamydoselachus*. The n. profundus (*n. pr*) in *Porolepis* (pp. 376—378; fig. 43) was a very strong nerve, dividing in the orbit into several branches, most of which passed forwards to the nasal cavity. It is specially characteristic, too, that it supplied the lateral parts of the snout. The n. profundus in *Chlamydoselachus* (p. 254; figs. 2, 3), on the other hand, does not break up into terminal branches in the orbit, and does not enter the nasal cavity. Nor does it take part in the innervation of the lateral parts of the snout. The lateral parts of the snout are supplied instead by the r. maxillaris V (*r. mx*), a nerve that was weakly developed in *Porolepis*, where it hardly extended into the snout.

The r. maxillaris V is accompanied in *Chlamydoselachus* by large vessels (*a. mx*, *v. fa*, figs. 2, 4), probably without equivalents in *Porolepis*. The v. cerebralis anterior must, if it was present in *Porolepis*, have had another course than in *Chlamydoselachus* (*v. ca*, figs. 2, 3).

The sensory canals of the snout have a fairly different course in *Porolepis* and *Chlamydoselachus*. The supraorbital canal (*soc*) passes in both dorso-medially to the external nostrils, but whereas in *Porolepis* (fig. 41; cf. fig. 33) it anastomoses anteriorly with the infraorbital canal antero-medially to the fenestra endonarina anterior, it curves backwards in *Chlamydoselachus* so as to anastomose with the infraorbital canal in the postero-lateral part of the snout behind the posterior nasal aperture. No equivalent to this latter part of the supraorbital canal is developed in *Porolepis.* The infraorbital canal (*ioc*) anostomoses in *Porolepis* anteriorly with the corresponding canal of the opposite side ventrally to the dorsal rostral process of the ethmoidal region (cf. foot-note on p. 258) and it does not form any hairpin curve ventrally to the said process as in *Chlamydoselachus.*

The palatoquadrate in *Chlamydoselachus* articulates with its antero-lateral part against the medial side of the ectethmoid process and with its antero-medial part, the orbital process, against an articular facet (*art. pr. o*, fig. 2) situated on the anterior part of the lateral face of the interorbital wall. This facet is bounded ventrally by a ridge, the palatobasal ridge (*ri. pal-b*, fig. 4; Allis 1923, pp. 126, 149), which constitutes the foremost part of the subocular shelf (the posterior part of this shelf is absent in adults, but is developed in embryos; Holmgren 1941, p. 10). As has been mentioned above, the palatoquadrate in *Porolepis* probably articulated with its antero-lateral part against the medial side of the processus ventro-lateralis, which may be compared to the ectethmoid process in *Chlamydoselachus.* With its antero-medial part the palatoquadrate in *Porolepis* articulated against the autopalatine fossa (*fo. aup*, fig. 37) which lies mainly on the anterior part of the lateral face of the interorbital wall and which is bounded ventrally by a ridge projecting laterally, the subocular shelf (pp. 362—363). It is thus obvious that the palatoquadrate was connected anteriorly with the endocranium in about the same way in *Porolepis* as in *Chlamydoselachus.* Behind the autopalatine fossa there is, however, in *Porolepis* a true basipterygoid process (*pr. bp*, pl. 3, figs. 1, 2; pl. 4; pl. 5, fig. 2) which projects laterally from the hindmost basal part of the interorbital wall and which is provided with a distinct articular facet for the palatoquadrate. This facet lies in the hinder part of the orbit just a little farther forward than the angle on the ventral side of the interorbital wall compared above (p. 358) to the basal angle in sharks. The facet thus has a position somewhat similar to that of the articular facet for the orbital process in several sharks, e. g. *Heptanchus* and *Squalus* (Daniel 1934, figs. 47, 48; Holmgren and Stensiö 1936, fig. 238 A; Holmgren 1941, fig. 24).

Thus the palatoquadrate in *Porolepis* had two articular connections with the lateral side of the interorbital wall, 1) a posterior one with the basipterygoid process, which is comparable to the connection between the orbital process of the palatoquadrate and the endocranium in such sharks as *Heptanchus* and *Squalus*, and 2) an anterior one with the autopalatine fossa, which is comparable to the connection between the orbital process and the endocranium in *Chlamydoselachus.* In addition there was probably in *Porolepis* 3) a connection between the antero-lateral part of the palatoquadrate and the processus ventro-lateralis, comparable to the connection between the palatoquadrate and the ectethmoid process in *Chlamydoselachus*. These three articular connections are in *Porolepis* but little or even indistinctly separated from each other and in fact there was thus in *Porolepis* as in *Eusthenopteron* (see p. 457) an almost continuous connection between the palatoquadrate and the endocranium from the basipterygoid process forwards as far as to the processus ventro-lateralis at the ventro-lateral corner of the postnasal wall. This condition may be primitive. It is not impossible that a similar extended articulation was present also in primitive sharks and that the very differently situated articular connections between the palatoquadrate and the endocranium in different sharks have evolved from such an extended articulation and are not strictly homologous throughout. A similar opinion has previously been advanced by HOLMGREN and STENSIÖ (1936, p. 319) whereas the majority of other writers (GAUPP 1905, p. 648; GOODRICH 1930, pp. 407—414; DE BEER 1937, p. 419) maintain that the orbital process is homologous in all sharks and that the articulation between it and the endocranium may shift along the ventral parts of the endocranium.

It is obvious from the comparisons now made that there are certain points of agreement between *Porolepiformes* (*Porolepis*) and sharks (*Chlamydoselachus*) as regards the position of the nasal capsules and the development of the internasal wall, the divisio prenasalis communis, the postnasal wall, and the articular connections of the palatoquadrate with the endocranium. In addition it is worthy of mention that the tectum orbitale is as a rule well developed in both *Porolepis* and sharks.

Most of the similarities just mentioned must certainly be regarded simply as general primitive characters. It is difficult to say whether the broad internasal wall and the position of the nasal capsules far from each other in the lateral parts of the ethmoidal region are primitive characters too, and I do not now want to express any definite opinion on that point. The fact that the internasal wall is narrow and the nasal capsules lie close to one another not only in certain sharks (e. g. *Heterodontus*, *Stegostoma*, *Chiloscyllium*; HOLMGREN 1941, p. 46; fig. 40) and other Elasmobranchs (Holocephalians, Placoderms; see pp. 388—389 below) but also in Osteolepiform Crossopterygians (p. 464; fig. 59), shows, however, that the internasal wall is fairly variable as to its development and that no great importance must be attached to its relative breadth.

The most important differences in the development of the snout between *Porolepiformes* and sharks are as follows. The fenestra endonarina posterior has a very different position in the two groups. The ala nasalis has no equivalent in *Porolepis*. The structure of the postero-lateral part of the nasal capsule is more complicated in *Porolepis* than in sharks. The sharks have no crista rostro-caudalis and the nasal cavity in them has no indication of a lateral recess. A choana was present in *Porolepis*, but no such formation is developed in sharks. The nasal sac in *Porolepis* was provided with a lateral diverticle. The nerves and vessels of the snout must clearly have been very differently developed in *Porolepis* from what they are in sharks and also the course of the sensory canals is different in the two groups. The palatoquadrate in *Porolepis*, contrary to what is the case in sharks, does not extend far forwards underneath the ethmoidal region, nor does it form any symphysis with that of the opposite side. Finally, the dentition in the snout of *Porolepis* is the normal one in Teleostome fishes and Tetrapods and not confined only to the oral faces of the jaws as in sharks.

The differences in the development of the snout in *Porolepiformes* and sharks are thus of fundamental importance, and it is fully obvious that the two groups cannot possibly be closely related.

The *Porolepiformes* will now be compared with certain other groups of Elasmobranchs.

The rays (see HOLMGREN and STENSIÖ 1936; HOLMGREN 1940; 1941; DE BEER 1937), which according to HOLMGREN (1940, pp. 258—259; 1941, pp. 78—79) belong to a lineage of their own different from that of the sharks, display no characters in the structure of their snout indicating a close kinship to the *Porolepiformes*.

Turning to the Holocephalians (ALLIS 1917; 1926; 1938; DE BEER and MOY-THOMAS 1935; DE BEER 1937; HOLMGREN and STENSIÖ 1936) we find that they differ very considerably from the *Porolepiformes* in the position of the nasal cavities far forwards and close together, in the presence of a nasal septum and ethmoidal canal and in several other respects. It is therefore likely that they are more distinct from the *Porolepiformes* even than the Selachians.

The fossil Selachians and Holocephalians are still very imperfectly known as regards the development of the snout (see MOY-THOMAS 1939) and they must therefore be disregarded in this connection. I shall here enter instead upon the Placoderms, which according to the views of several recent writers are Elasmobranchs in a wide sense or are comparatively closely affined to Elasmobranchs (WOODWARD 1924; 1932, p. 42; 1938; STENSIÖ 1925 a, pp. 187—189; 1931, pp. 158—160; 1934; 1942; 1943; HOLMGREN and STENSIÖ 1936, p. 324; STENSIÖ and JARVIK 1939; SÄVE-SÖDERBERGH 1934; 1937 a; GROSS 1937 a; HEINTZ 1939; HOLMGREN 1940, pp. 247—252).

Among the Arthrodires the ethmoidal region is fairly well known especially in *Pholidosteus* (STENSIÖ 1934; cf. STENSIÖ 1925 a; 1942; HILLS

1936). It is not completely preserved, but in the main it is as follows (cf. Stensiö 1934, pp. 5—13). Taken as a whole it is short and broad. The "antorbital process" is absent and the postnasal wall has an unusual longitudinal position and passes over into the interorbital wall as well as the lateral nasal wall without any distinct boundary. The foremost part of the cranial cavity is divided into two halves by a median vertical rostro-caudal wall. The anterior end of each half of the foremost part of the cranial cavity is separated from the nasal cavity of its side by a thin transverse bone lamina pierced by a number of small foramina. The nasal cavity is situated in the very rostral end of the ethmoidal region. It is separated from the corresponding cavity of the opposite side by a comparatively thin nasal septum which forms a straight anterior prolongation of the median wall in the foremost part of the cranial cavity. The prenasal wall was either absent or very imperfectly developed. The nasal cavity opened straight forwards through an opening which must be regarded as a fenestra endonarina communis (cf. Stensiö 1942, figs. 3 A, B, 5, 7, 10). Below this opening there is a notch in the solum nasi which according to Stensiö possibly represents the nasal fontanelle in Selachians. A similar notch is found in the anterior margin of the tectum nasi.

These data suffice to show that *Pholidosteus* and the Arthrodires in general are very different from *Porolepis* with regard to the ethmoidal region. As to the snout, *Porolepis* and Arthrodires differ much more from each other than do *Porolepis* and *Chlamydoselachus.*

In the *Antiarchi* the endocranium has not been found preserved and but little is therefore known concerning the ethmoidal region in this group (see Stensiö 1931, pp. 27—30, 54—57, figs. 2 A, C, 10; 1943). The paired nasal opening lay far behind the rostral end of the head close in front of the eye and close to that of the other side. It is thus fully evident that as regards the ethmoidal region and the snout as a whole the *Antiarchi* must have differed widely from the *Porolepiformes.*

It may be added here that the pattern of the dermal bones of the snout and of the rest of the skull in both Arthrodires and *Antiarchi* is such that it cannot be directly compared to that in *Porolepiformes* and other Crossopterygians (cf. Holmgren and Stensiö 1936, p. 334). As recently shown by Holmgren (1940, pp. 247—252), the mesenchymatic areas described by him in shark embryos are on the whole disposed as the dermal bones in Arthrodires. For this and other reasons Holmgren is inclined to consider that these areas are vestiges of dermal bones and that the ancestors of the sharks were provided with a dermal head-skeleton of a fundamentally Arthrodiran type.

The above account clearly shows that as regards the snout there are no characters indicating that the *Porolepiformes* are in any way closely related to the Elasmobranchs.

b. Comparison with Brachiopterygii (Polypterus).

The snout of *Porolepis* differs from that of *Polypterus* (see pp. 256—265; figs. 5—9, 84) inter alia in the following respects. The nasal cavities lie far apart; the internasal wall is broad and houses the ethmoidal part of the cranial cavity; a cavum internasale is developed; the ethmoidal commissure of the infraorbital canals lies ventrally to the rostral tip of the endocranium; the fenestra endonarina anterior and posterior are widely separated; there is a fenestra endochoanalis; there is a lateral recess in the nasal cavity and a crista rostro-caudalis forms the dorsal boundary of this recess; Seydel's palatal process is developed; there is no antero-medial recess in the nasal cavity; the bulbus olfactorius lies ventro-laterally to the posterior part of the hemisphere of its side; the n. profundus did not accompany the r. ophthalmicus lateralis; the n. profundus was strongly developed and in all probability supplied also the lateral parts of the snout; the n. profundus broke up in the orbit inter alia into a strong medial and one or more lateral nasal branches; the medial one of those branches broke up into numerous small branches in the nasal cavity; the r. maxillaris V was weakly developed and probably hardly reached the snout; there was no foramen or canal in the ventral part of the lateral nasal wall for the r. buccalis lateralis and the r. maxillaris V.

It is quite evident that the structure of the snout is very different in *Porolepis* and *Polypterus.*

c. Comparison with Actinopterygii.

Recent Actinopterygians (pp. 265—270; fig. 10) differ so distinctly from *Porolepis* as regards the snout that it is not necessary to enter upon a detailed comparison. That there cannot be a close kinship between *Porolepis* and Actinopterygians is shown by the following characters in the Actinopterygians: The presence of a nasal septum; the absence of a fenestra endochoanalis and a true choana; the weak development or absence of anterior, lateral and dorsal nasal walls; the absence of Seydel's palatal process; the absence of the crista rostro-caudalis; the different nerve and vascular supply of the snout; and finally also in all probability considerable differences in the development of the forebrain.

The ethmoidal region of the primitive fossil Actinopterygians (see Watson 1925; 1928; Case 1937; Dyne 1939; Nielsen 1942, pp. 84—86, 96, 315—319; figs. 7, 9—13, 17, 21, 60, 62, 65) is also developed quite differently to that of the *Porolepiformes.* Also in the development of the dermal bones and in the course and disposition of the sensory canals we find considerable differences between these two groups (cf. pp. 345—346, 615—616).

d. Comparison with Dipnoi.

Porolepis differs from recent Dipnoans (pp. 270—284; figs. 11—15) as to the snout above all in the following respects.

The endocranial parts and the dermal bones are much better and more completely developed. The nasal capsules lie much further apart and no nasal septum is developed. The internasal wall is broad and houses the foremost part of the cranial cavity and the paired cavum internasale. The nasal walls are all well developed, even the solum nasi and the postnasal wall. The fenestrae endonarinae anterior and posterior lie on the lateral side of the snout (not in the roof of the mouth; see p. 280; cf. fig. 13). There is a fenestra endochoanalis, and a true choana was developed. The nasal cavity presents a lateral recess and a rostrocaudal crista. Seydel's palatal process is present. The palatoquadrate is developed as an independent element articulating with the ethmoidal region. The nasal sac was provided with a lateral diverticle situated between the posterior external nostril and the choana, a diverticle comparable to "Jacobson's organ" in Urodeles. The nasal sac was devoid of a diverticle dorsally to the posterior external nostril (cf. p. 280 above). The bulbus olfactorius lay ventro-laterally to the posterior part of the hemisphere of its side. The n. profundus was much more strongly developed and supplied also the lateral parts of the snout. Its medial nasal branch passed through the nasal cavity and there gave off numerous fine dorsal branches. The r. maxillaris V was weakly developed and hardly reached the snout. The ethmoidal commissure of the infraorbital canals lies ventrally to the tip of the ethmoidal region. The supraorbital canal passes medially to the tectum nasi, which bulges slightly upwards, anastomoses anteriorly with the infraorbital canal of its side and is not connected with that of the opposite side by any transverse commissural canals (cf. GOODRICH 1930, fig. 722; HILLS 1933, fig. 3).

The differences here enumerated demonstrate beyond question that *Porolepiformes* and recent Dipnoans are very different in the development of the snout. The snout displays no points of agreement indicating any close relationship between these two groups.

The fossil Dipnoans (GOODRICH 1909, pp. 238—242, figs. 208—210 A; 1925; WATSON and DAY 1916; WATSON and GILL 1923; SÄVE-SÖDERBERGH 1932 a, figs. 20, 21; HILLS 1933; HOLMGREN and STENSIÖ 1936, pp. 363—372, figs. 279—286; ROMER 1936; FORSTER-COOPER 1937; GRAHAM-SMITH and WESTOLL 1937) seem to agree in the structure of the snout essentially with the recent forms. Even in the geologically oldest forms, *Dipnorhynchus* (HILLS 1933) and *Dipterus valenciennesi* (*D.* "*platycephalus*", Watson and Day 1916, fig. 6; Graham-Smith and Westoll 1937, fig. 8 d) from the middle Devonian, the incurrent and probably also the excurrent nostril lay on the ventral side of the snout in a similar way as in recent forms. At least in *D. valenciennesi* the vomer lies close to that of the opposite side and forms with it a long median suture, a condition indicating that no cavity corresponding to the cavum internasale in *Porolepis* is present. Also in the development and forward extent of the parasphenoid we find considerable differences between the *Porolepiformes* and the oldest Dipnoans.

As may easily be gathered from what has been said above the *Porolepiformes* differ considerably from the Dipnoans as regards the development of the snout. As far as I can see there is nothing in the snout to support the belief that the *Porolepiformes* and Dipnoans are closely related to each other.

e. Comparison with Urodela.

It could be established above (pp. 376—379) that the general nerve and vascular supply of the snout of *Porolepis* in all probability was as follows: 1) The n. profundus was very strongly developed; 2) this nerve supplied not only the rostral end and the dorsal side of the snout but also the lateral parts; 3) the r. maxillaris V was weakly developed and apparently terminated at or near the antero-ventro-lateral corner of the orbit; it thus hardly extended forwards into the snout; and 4) no large vessels passed to or from the snout along the postero-latero-ventral parts of the ethmoidal region, all the principal vessels of the snout having a more medial course so that they left or emerged into the antero-medial part of the orbit. As to these four fundamental characters *Porolepis* agrees in a most striking way with the Urodeles (cf. pp. 302—308), whereas it differs completely from all other recent vertebrate groups here treated, viz. Elasmobranchs, Brachiopterygians, Actinopterygians, Dipnoans, and Anurans. In the latter groups the n. profundus is not particularly strong; the lateral parts of the snout are supplied by the r. maxillaris V, which is strongly developed and extends far forwards into the snout. In addition the lateral parts of the snout are supplied and drained by large vessels accompanying the r. maxillaris V to and from the postero-ventral corner of the orbit. Also the Osteolepiform and Coelacanthiform Crossopterygians (cf. pp. 476—481, 576—579) resembled the recent groups enumerated as regards the characters here under consideration. With regard to the general nerve and vascular supply of the snout the Porolepiform Crossopterygians and Urodeles are thus quite unique among lower Gnathostome vertebrates. The amazingly close agreement between them in these respects is therefore highly interesting and cannot possibly be without phylogenetical importance.

The agreement between Porolepiform Crossopterygians and Urodeles as to the innervation and vascular supply of the snout is not, however, confined to the general features just referred to, but is much greater and goes even very far as to details.

A comparison between the course of the n. profundus in *Porolepis* as restored above (pp. 376—378; fig. 43) and the course of the corresponding nerve in Urodeles (*Salamandra*; pp. 302—304; figs. 20, 21) discloses the following facts.

The n. profundus (*n. pr*) in *Salamandra* and other Urodeles gives off some dorsal branches (*n. prd*) which are distributed to the skin above and anteriorly to the eye. Of these branches, which have a fairly varying course, one may accompany the r. ophthalmicus lateralis as in *Amphiuma*. These branches may in *Porolepis* have been represented by the presumed branches *r. pras* and *r. prdl*, the former of which accompanied the r. ophthalmicus lateralis.

In *Salamandra* the n. profundus breaks up, in the middle part of the orbit, into three terminal branches, the medial, lateral and ventral ones. Of these branches the medial and strongest one (*n. 5a. M*) together with the ventral one (*n. 5a. V*) passes through the wide medial profundus foramen (*f. prm*, figs. 16 C, 20) to the nasal cavity, whereas the lateral one (*n. 5a. L*) traverses one of the lateral profundus foramina (*f. prl*). Another of the lateral profundus foramina gives passage to a nerve branch formed by the anastomosing of a small branch of each of the medial and lateral profundus branches. The presence in *Porolepis* of a very wide medial (*c. prm*, figs. 36 B, 37 B, 42) and one or more lateral (c_1prl, c_2prl) profundus canals situated as the profundus foramina in *Salamandra*, shows that the n. profundus in *Porolepis* divided fairly far behind the postnasal wall into at least two main branches, a very strong medial one (*r. prm*), which corresponded to the medial terminal branch in *Salamandra*, and a lateral one which represented the lateral terminal branch in the last-mentioned form. Whether in *Porolepis* there were any branches equivalent to the ventral terminal branch and the anastomose branch in *Salamandra* could not be established. Just where it breaks up into its three terminal branches the n. profundus in *Salamandra* gives off a fine dorsal branch (cf. Francis 1934, pl. 13, fig. 57) which, judging from its position and course, may be represented in *Porolepis* by the presumed branch *r. prd*.

Within the nasal cavity the medial terminal profundus branch runs forwards in *Salamandra* and other Urodeles dorsally to the olfactory nerve and the dorso-medial parts of the nasal sac, and breaks up into numerous fine branches (*n. 5a. Ma*, *n. 5a. Md*) which leave the nasal cavity through numerous foramina in the medial parts of the tectum nasi and in the adjacent parts of the medial and anterior nasal walls (pp. 289, 291—292; *f. 5a. Ma*, *f. 5a. Md*, figs. 16 B, D, 17 A). In *Porolepis* it is obvious that the medial terminal profundus branch must also have passed dorsally to the olfactory nerve and the dorso-medial parts of the nasal sac. The presence of numerous canals (*c. prt*, figs. 39, 42, 43) in the medial parts of the tectum nasi and in the adjoining parts of the medial and anterior nasal walls shows that the medial terminal profundus branch in this form must also have broken up into a large number of fine branches (*rr. prt*) exactly as in Urodeles. Finally, it is also evident that these branches had a similar course and distribution as the corresponding ones in Urodeles.

The canal *c. cut. va*? (p. 375; figs. 39, 42, 43) in *Porolepis* has such a position and course that it may very well have given passage to a profundus branch corresponding to the one in *Desmognathus* (p. 291) that pierces the posterior part of the medial nasal wall and goes to the cavum internasale. Whether the canal *c.cut. va*? in *Porolepis* was possibly traversed also by a vessel — a vein collecting the blood from the dorso-medial parts of the roof of the snout and accompanying the n. olfactorius backwards — could not be ascertained (cf. p. 547). As far as I can find no such vein is known of in Urodeles (see e. g. ROOFE 1935).

The branch, *r. pror*, of the n. profundus in *Porolepis* that presumably traversed the orbitorostral passage (pp. 375—376) medially to the choana and ventrally to the lateral parts of the nasal sac as well as the probable twig or twigs *r. prvl* given off from it, appear to lack equivalents in *Salamandra*. In other Urodeles, e. g. in *Siren* (NORRIS 1913, pp. 279—282, 293; figs. 4—7, 15; pl. 1), however, there is a profundus branch (*op-pal. m*) with a corresponding course and with a lateral twig (*op. 4 l*). This profundus branch in *Siren* is accompanied by a buccalis branch (*buc. 2*) which supplies the foremost sensory organs of the infraorbital line (p. 305; cf. COGHILL 1906, p. 255).

As no separate buccalis canal has been found in *Porolepis* it is conceivable that the r. buccalis lateralis broke up in the orbit, as in *Siren* (p. 305), into terminal branches, one of which went forwards through the orbitorostral passage to innervate the anterior sensory organs of the infraorbital line.

In those Urodeles in which it persists in adults, the r. ophthalmicus lateralis passes on the dorsal face of the ethmoidal region underneath the dermal bones and dorso-medially to the nasal sac and the external nasal opening (cf. p. 302), as it probably did in *Porolepis*. In order to reach the dorsal face of the ethmoidal region the r. ophthalmicus lateralis in *Porolepis* traversed a canal (*c. o. lat*, figs. 36 B, 37 B) in the postnasal wall. The absence of such a canal in Urodeles is certainly due only to the relatively slight development of their skeleton.

The r. palatinus VII obviously had a similar course in relation to the vomer in *Porolepis* and Urodeles. In *Porolepis* it was enclosed in the postero-medial part of the vomer in a short palatine canal (*c. pal*, fig. 37 A). In certain Urodeles, e. g. *Ambystoma tigrinum* (Wintrebert 1922, figs. 44, 45, *ep*), there is a notch for it in the medial part of the posterior margin of the vomer, thus at the same spot as the posterior orifice of the palatine canal in *Porolepis*.

Owing to the fact that the snout in *Porolepis* is very strongly ossified, its nerves and vessels, except those passing in the roof of the mouth and in the skin, were all partly or throughout situated in canals in the skeleton. In restoring the nervous system of the snout in *Porolepis* it was postulated that all the canals had housed nerves, except, of course, the sensory canals. The fact that the nervous system as restored on this postulation agrees almost in every detail with that in recent Urodeles obviously strongly supports the correctness of the restoration made.

As, with the exception of the sensory canals, all the canals of the snout in *Porolepiformes* thus in all probability housed nerves, the vessels had no large separate canals of their own, but in the main accompanied the nerves. So everything seems to indicate that also the vascular system of the *Porolepiformes* was developed in a way similar to that of the Urodeles.

If the nervous and vascular systems of the snout in *Porolepiformes* were thus developed as in Urodeles, the conclusion readily suggests itself that *Porolepiformes* and Urodeles are closely related forms and that the Urodeles are derived from *Porolepiformes* or at least from ancestors very closely akin to them. As we shall see, this conclusion is strongly supported both by the development of the skeleton and by other conditions in the snout of the *Porolepiformes*.

The forebrain in *Porolepiformes* (p. 364; fig. 43; cf. fig. 38) was broader than the diencephalon. The hemispheres were oblong and lay close to one another. The bulbus olfactorius was conceivably situated close ventro-laterally to the hemisphere of its side and was thus presumably widely separated from the one of the opposite side. In all these characters *Porolepis* was Urodele-like (pp. 301—302, fig. 21). However, in *Porolepis* the bulbus olfactorius lay close to the posterior part of the hemisphere, whereas in Urodeles it lies close to the anterior part of the corresponding part of the forebrain. If the Urodeles have evolved from Porolepiform ancestors, a change in the position of the bulbus olfactorius must be expected to have taken place in Urodeles. It is of great interest to find, therefore, that in the larvae of Urodeles the bulbus olfactorius lies further posteriorly in relation to the anterior end of the hemisphere than in the adults (fig. 19; cf. foot-note 1 below; HERRICK 1910, pp. 416, 421; 1938, p. 212, figs. 15, 17, 23; 1938 a, p. 20; SÖDERBERG 1922, pp. 111—113; SUMI 1926, p. 218). This condition is obviously due to the position of the hemispheres in the larvae. In the larvae these divisions of the forebrain extend far forwards between the nasal sacs quite as they must have done in *Porolepis*, but are then completely or almost completely retracted from the ethmoidal region.[1]

The internasal wall is broad both in *Porolepis* (figs. 39, 43) and *Salamandra* (fig. 16). In both forms it lodges the ethmoidal part of the cranial cavity, and in front of this it is provided, on its ventral side, with a large cavum internasale opening ventrally (*cav. in*) and bounded laterally by the anterior parts of the medial nasal wall. The cavum internasale, which extends far dorsally into the internasal wall, is continuous anteriorly with another space, the cavum prenasale, which lies in the short and broad divisio prenasalis communis. As regards the main features of the internasal wall and the divisio prenasalis communis *Porolepis* and *Salamandra* thus agree with each other, whereas with regard to the detailed development of these skeletal formations they present several differences. The most important differences are the following: 1) The cavum internasale and cavum prenasale are paired in *Porolepis*, unpaired in *Salamandra*; 2) the wall between the ethmoidal part of the cranial cavity and the nasal cavity, that is to say the hinder portion of the medial nasal wall, is thick in *Porolepis*, and in order to reach the nasal cavity the olfactory nerve therefore had to pass a long canalis olfactorius; in *Salamandra* the corresponding wall is thin and perforated by a fenestra olfactoria; 3) the space in *Porolepis* occupied by the paired cavum internasale and the internasal ridge (*ri. in*) is broader than the unpaired cavum internasale in *Salamandra*; 4) the divisio prenasalis communis is much more completely developed in *Porolepis* than in *Sala-*

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[1] According to a statement by STADTMÜLLER (1936, p. 560) the brain in "den niedersten Perennibranchiaten" also in the adults retains its primitive position between the nasal sacs. This statement does not seem to be true. Both *Proteus* (BENEDETTI 1933, p. 48, pl. 1, figs. 1—5) and *Necturus* (KINGSBURY 1895, pp. 145—146; pl. 9, figs. 1, 2) have long olfactory nerves projecting anteriorly, which shows that the brain in them, contrary to what is stated by STADTMÜLLER, must end far behind the nasal sacs (cf. WIEDERSHEIM 1877, pl. 21, fig. 41). On the other hand, in the adult *Siren* (NORRIS 1913, fig. 2) enumerated by STADTMÜLLER among the forms with a retracted brain, the forebrain distinctly extends forwards between the posterior parts of the nasal sacs, about as must have been the case in *Porolepis*. An interesting feature in *Siren* is also that the bulbus olfactorius lies comparatively far behind the tip of the hemisphere.

mandra and the cavum prenasale is smaller. No processes corresponding to the processus prenasalis inferior lateralis and the processus prenasalis superior medius in *Salamandra* are developed in *Porolepis.*

Let us now consider each of these four differences in the light of conditions in other Urodeles.

1) In the majority of the Urodeles, as in *Salamandra*, the cavum internasale and the cavum prenasale are unpaired and neither in larvae nor adults of these Urodeles are there any traces whatever of an equivalent to the internasal ridge (*ri.in*, figs. 36 A, 37 A, 39, 43, 44, 46 A) of the *Porolepiformes.* As pointed out above (p. 286), however, the cavum internasale is divided incompletely in certain Urodeles (*Amphiuma*, etc.) into a right and a left half by a median unpaired plate of cartilage, the cartilago infranasalis (*cart.ifn*, fig. 46 B). Judging from the position of this plate of cartilage it probably represents a vestige of the internasal ridge of the *Porolepiformes.*

2) In the majority of Urodeles the wall between the ethmoidal part of the cranial cavity and the nasal cavity is, relatively, as thin as in *Salamandra.* However, in certain forms, e.g. *Siredon* (WIEDERSHEIM 1877, pl. 21, fig. 28; GROTE 1926, p. 461), this wall is comparatively thick and the opening in it for the olfactory nerve is described as an olfactory canal.[1] This olfactory canal is shorter than that in *Porolepis*, but the difference is not particularly large. *Siredon* is thus in this respect intermediate between *Salamandra* and the majority of Urodeles on the one hand and *Porolepiformes* on the other.

As pointed out above the brain in Urodeles is retracted from the ethmoidal region during the ontogeny. Simultaneously with the retraction of the brain the nasal cavities increase in size in a medial direction at the cost of the cavum internasale (cf. p. 398). The two phenomena just mentioned lead together to a change in the position of the fenestra olfactoria from an almost sagittal to an almost transverse position (cf. inter alia AOYAMA 1930, p. 159). If in a *Porolepis*-like form the nasal cavities had widened by an extension in a medial direction in connection with a withdrawal of the brain from the ethmoidal region, this would obviously have caused a thinning of the wall between the nasal cavity and the ethmoidal part of the cranial cavity (cf. fig. 43). It would also have led to a shortening of the canalis olfactorius and to a change in the position of the anterior (nasal) opening of this canal, so that its anterior opening would have become mainly transversely situated. It is thus obvious that the differences between *Porolepis* and *Salamandra* under 2) are not of a profound nature. They have all arisen secondarily in Urodeles and the phenomena leading to them are to a large extent recapitulated in the ontogenic development of the Urodeles.

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[1] In certain Urodeles, as *Necturus* (*Menobranchus;* WIEDERSHEIM 1877, pp. 520—521; pl. 21, fig. 41), the olfactory nerve traverses a comparatively long canal. This canal is formed of dermal bones, however, and is therefore not homologous to the canalis olfactorius in *Porolepis.*

3) In *Salamandra* and the majority of other Urodeles the cavum internasale (*cav. in*, figs. 16 B, 17 B, 18 A) is generally considerably narrower than the foremost part of the cranial cavity. A large variation is, however, met with in Urodeles as regards the relative breadth of the cavum internasale. If we disregard the dermal bones covering it, this cavity is in *Salamandrina* (Wiedersheim 1877, pl. 21, fig. 26) of a similar breadth posteriorly as the adjacent part of the cranial cavity, whereas anteriorly it is broader than that part of the cranial cavity. In *Salamandrina* it is thus of a corresponding breadth in relation to the cranial cavity as the two cava internasalia in *Porolepis* together (fig. 43). It thus follows that no special importance must be attached to the differences between *Porolepis* and Urodeles set forth under 3). It is most interesting to note in this connection, that, as has been mentioned above, the nasal cavities in Urodeles become larger during the embryological development and that this widening of the nasal cavities takes place in a medial direction so as to cause a reduction in breadth of the cavum internasale. Stadtmüller (1924, p. 184) has found that in *Salamandra* the breadth of the cavum internasale was 17 % of the total length of the skull in a 3.5 cm larva, but only 11 % in a metamorphosing larva. As is seen from a figure given by Stadtmüller (fig. 16 D in this work) the width of the cavum internasale in the 3.5 cm larva approximately corresponds to the foremost part of the cranial cavity and the relative width agrees with the two cava internasalia in *Porolepis*. Accordingly the decrease in width to which the cavum internasale in *Salamandra* is subjected during the ontogeny is clearly a secondary process, which is a recapitulation of the phyletic development.

4) The cavum prenasale in *Salamandra* is bounded postero-laterally, on either side of the cavum internasale, by the thin prenasal wall and dorso-medially and antero-dorso-medially by the anterior part of the processus prenasalis superior medius (*pr. psm*, figs. 16 A, B, 20). Its antero-lateral and ventral boundaries, both of which are incomplete, are formed by the pars facialis (Pmx_2) and pars palatina (Pmx_3) of the "premaxillary". The pars facialis rests against the dorsal part of the prenasal wall and is supported most ventrally by the paired processus prenasalis inferior lateralis (*pr. pil*) which points forward and somewhat inward. This process, the unpaired processus prenasalis superior medius and the paired prenasal wall constitute together the skeleton of the divisio prenasalis communis. The relatively small cavum prenasale in *Porolepis*, that is to

say the foremost part of the space described (p. 364) as the cavum internasale (*cav. in*, figs. 36 A, 37 A, 39, 43, 46 A), is bounded anteriorly, dorsally and laterally by the divisio prenasalis communis. The "premaxillary" in *Porolepis* (rostro-premaxillary or naso-rostro-premaxillary; cf. p. 347) consists morphologically — as the "premaxillary" in Urodeles (p. 413) — of three divisions, pars dentalis, pars facialis, and pars palatina, of which the pars facialis covers the external face directed antero-laterally and the pars palatina the antero-lateral part of the lower face of the divisio prenasalis communis. As these three divisions of the "premaxillary" in *Porolepis* are undoubtedly homologous with the correspondingly termed ones in Urodeles (cf. p. 413) it is evident that the divisio prenasalis communis in *Porolepis* differs from that in *Salamandra* only by being more completely developed and ossified throughout. By a process of reduction it may therefore very well have given rise to a similar divisio prenasalis communis as that found in *Salamandra* and Urodeles in general. If we assume that together with an adjoining part of the internasal wall it had become resorbed with the exception of a) the postero-lateral portion of the prenasal wall situated immediately antero-medially to the nasal cavity (fig. 43), b) the ventral portion of the part that bounds the cavum prenasale antero-laterally and lies postero-laterally to and supports the ventral part of the pars facialis of the "premaxillary" (fig. 36 A), and c) a thin antero-dorso-median portion, the cavum prenasale would be almost exactly as in *Salamandra*. The remaining parts of the divisio prenasalis communis would then in all essentials agree with the following ones in *Salamandra*: a) the paired prenasal wall, b) the paired processus prenasalis inferior lateralis, and c) the unpaired processus prenasalis superior medius. The differences between *Porolepis* and *Salamandra* as to the development of the divisio prenasalis communis are thus in all probability due to a regressive development in the latter form. A strong support for this opinion is found in the fact that the divisio prenasalis communis is much more strongly developed in Hynobiids[1], which are generally maintained to be the most primitive recent Urodeles, than in *Salamandra*. As we have seen (pp. 285—286), in Hynobiids the roof of the cavum internasale is complete and the processus prenasalis superior medius (cf. *pr. psm*, fig. 46 B) short and broad and entirely or almost entirely situated in the divisio prenasalis communis. It may be added that in some of them, e. g. *Pseudosalamandra* (Chung 1931, pl. 12, fig. 16), the processus prenasalis inferior lateralis is strikingly short and thick (cf. *pr. pil*, fig. 46 B). With regard to the divisio prenasalis communis the Hynobiids are thus to some extent intermediate between *Porolepis* and *Salamandra*.

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[1] According to DUNN (1923) and NOBLE (1931) the family *Hynobiidae* comprises only the genera *Hynobius* (*Pseudosalamandra, Ellipsoglossa, Salamandrella*), *Pachypalaminus, Onychodactylus* (*Geomolge*), *Batrachuperus*, and *Ranodon*. In agreement with CHUNG, YATABE, and others, I have for certain of the species retained the earlier generic names, viz. *Pseudosalamandra* for *Hynobius kimurai, Salamandrella* for *H. keyserlingii*, and *Geomolge* for *Onychodactylus fischeri*.

It is thus evident that there are fundamental points of agreement between *Porolepiformes* and Urodeles in the development of the internasal wall and the divisio prenasalis communis. It is particularly interesting to note that in these parts of the ethmoidal region the *Porolepiformes* show a much closer agreement with primitive Urodeles (Hynobiids and Cryptobranchids) and larvae of Urodeles than with the adults of more advanced forms, such as *Salamandra*. What has just been set forth strongly supports the opinion advanced above that *Porolepiformes* and Urodeles are closely related forms and that the Urodeles are derived either from primitive *Porolepiformes* or from ancestors closely related to these. The following conclusions thus seem to be fully justified: 1) The cava internasalia and prenasalia of both sides in *Porolepis* are together homologous to the unpaired cavum internasale and unpaired cavum prenasale respectively in Urodeles; 2) the internasal ridge in *Porolepis* is the homologue of the cartilago infranasalis of Urodeles; 3) the processus prenasalis inferior lateralis in Urodeles is derived from the ventral portion of those parts of the internasal wall and divisio prenasalis communis in *Porolepis* that form the antero-lateral boundary of the cavum internasale and cavum prenasale of its side; and finally, 4) the processus prenasalis superior medius in Urodeles has arisen from the antero-dorso-median part of the divisio prenasalis communis and the adjoining dorso-median part of the internasal wall in *Porolepis*.

The cavum internasale and the cavum prenasale in Urodeles lodge the intermaxillary gland (p. 300; *gl. imx*, fig. 18). This gland opens ventrally in the roof of the mouth cavity through one or more ducts (Seifert 1932). Dorsally it reaches upwards to the dermal bones of the skull-roof and through perforations in the skull-roof it may sometimes extend as far as to the skin (Wiedersheim 1876, pl. 1; Fahrenholz 1937, p. 135). It thus extends in a dorso-ventral direction throughout the depth of the ethmoidal region. As has been shown above (pp. 366—367), the cavum internasale (including the cavum prenasale) in *Porolepiformes* cannot possibly have been developed for any of the large tusks of the lower jaw. On account of its position and homology and in view of the fact that it extends far upwards into the ethmoidal region and opens ventrally towards the mouth cavity, it is extremely likely that it housed a gland corresponding to the intermaxillary gland in Urodeles. The fact that the cavum internasale (including the cavum prenasale) is paired in *Porolepiformes* implies that their intermaxillary gland must have been paired too. On the other hand the intermaxillary gland in Urodeles forms a single glandular formation. Its embryonic development is but slightly known, but the researches treating it from that point of view (I. W. Wilder 1913, p. 316; Schultze 1937, p. 485; Stadtmüller 1924, p. 184; cf. Fukuchi 1936 a) seem to favour the opinion that it arises from an unpaired primordium. The fact that its secretion as usual passed down to the mouth cavity through several ducts, shows, however, that it probably constitutes a complex gland which may have been formed by a congregation of several primordia (cf. Fahrenholz 1937). It is of interest in this connection that the intermaxillary gland arises from a paired primordium at least in one Anuran form, *Bufo*, and that in addition it is paired in the adult *Xenopus* (see p. 322).

The nasal cavity is both in *Porolepiformes* and Urodeles widely separated from that of the opposite side by the broad internasal wall. Both in *Porolepis* (figs. 39, 42, 43, 46 A) and Urodeles (figs. 16—18, 46 B, C) it has a principal chamber and a lateral recess. Its anterior and antero-lateral parts are completely devoid of the subdivision into compartments that is so characteristic of Anurans, and, as we shall see, also of Osteolepiform Crossopterygians. Nor is there any medial or antero-medial recess. The lateral wall of the nasal cavity is pierced both in *Porolepis* and Urodeles by a fenestra endonarina anterior and a fenestra endonarina posterior, whereas the ventral wall of this chamber presents a fenestra endochoanalis. The lateral recess (*re. l*) is very similarly developed in *Porolepis* (p. 368; figs. 36 B, 37 B, 39, 40 A, C, 42 A—C, 46 A) and Urodeles (p. 292; figs. 16 C, 18 C). In both it lies in the postero-ventro-lateral part of the nasal cavity and is anteriorly and medially in open communication with the principal chamber, whereas posteriorly it opens into the mouth cavity. It is bounded ventrally by the postero-lateral part of the solum nasi and laterally and dorso-laterally by the lateral nasal wall. The dorsal boundary of the recess in both *Porolepis* and Urodeles is formed by a crest, the crista rostro-caudalis (*ri. w. al*), which projects medially into the nasal cavity from the lateral nasal wall and stretches from somewhere postero-ventrally to the fenestra endonarina anterior backwards as far as the posterior end of the nasal cavity. Along the dorsal margin of this crest there is a rostro-caudal groove in the medial face of the lateral nasal wall. This groove, denoted in *Porolepis* with the letters *gr. ntp* but referred to in Urodeles (p. 295) as the internal nasolachrymal groove, is in Urodeles caused by the nasolachrymal duct, whereas in *Porolepis* it was developed for the posterior external nasal tube. The part of the solum nasi that forms the ventral boundary of the lateral recess is produced posteriorly in both *Porolepis* and Urodeles into an obtuse process projecting backwards, Seydel's palatal process (*pr. S* figs. 16 B, 40 D), which is separated from the adjacent part of the lateral nasal wall by a shallow notch, the incisura ectochoanalis (*i. ech*).

As may be gathered from the above comparison, the similarly termed formations of the nasal cavities in *Porolepis* and Urodeles agree so completely that they cannot possibly be parallelisms, but must be due to a close relationship between *Porolepiformes* and Urodeles. We are forced to the conclusion, therefore, that the principal chamber, lateral recess, fenestra endonarina anterior (concerning the fenestra endonarina posterior see pp. 403—411), fenestra endochoanalis, crista rostro-caudalis, Seydel's palatal process, and the incisura ectochoanalis are homologous formations in the two groups. Everything thus tends to show that also the groove *gr. ntp* in *Porolepis* is the strict equivalent of the internal nasolachrymal groove in Urodeles, and hence it follows that the nasolachrymal duct in Urodeles must be the strict homologue of the posterior external nasal tube in *Porolepiformes*. It is also obvious that the nariodal bone (*Nd*, figs. 18 A, B, 46 B, C) in Urodeles is simply a part of the lateral nasal wall, in which the phylogenetically primitive bone tissue persists, whereas the other parts of the ethmoidal region have secondarily failed to ossify. That the nariodal bone in Urodeles is a true cartilage-bone is thus clear beyond question (cf. p. 294).

The fundamental points of agreement in the development of the nasal cavity here demonstrated must mean, of course, that the nasal sac in *Porolepis* (*sac n*, fig. 43) was on the whole as the nasal sac in Urodeles (pp. 300—301; figs. 18—19). It is thus very likely that it consisted of a main part and a lateral diverticle. The main part opened outwards through a short anterior external nasal tube (*nta*) and downwards into the mouth cavity through an internal nasal or choanal tube. The lateral diverticle must have consisted of two divisions, a dorsal (anterior) one which lay above the anterior part of the crista rostro-caudalis and was continued backwards by the posterior external nasal tube, and a ventral (posterior) one which was situated ventrally to the crista rostro-caudalis in the lateral recess. Since the lateral recess opens posteriorly into the mouth cavity, it is very likely that the ventral division of the lateral diverticle was developed almost exactly as the corresponding division in Urodeles. Accordingly its lumen (sinus lateralis nasi) was in all probability in open communication with the mouth cavity posteriorly by means of a sulcus maxillo-palatinus, which was bounded ventrally by a fold of mucous membrane, a plica palatina, supported by Seydel's palatal process. It is also quite conceivable that the ventral division of the diverticle was lined with sensory epithelium and formed a strict equivalent of the so-called Jacobson organ in Urodeles.

With regard to the fenestra endonarina posterior, the fenestra endochoanalis, and the posterior external nasal tube and nasolachrymal duct *Porolepis* and Urodeles present certain differences which will now be discussed.

The fenestra endonarina posterior in *Porolepis* (*fe.enp*, fig. 40 A, C) lies in the postero-ventral part of the lateral nasal wall. It is relatively large, and continuous ventrally with the fenestra endochoanalis (*fe.ench*, fig. 40 D) which is a comparatively small opening in the postero-lateral part of the solum nasi. On the other hand, the fenestra endonarina posterior in Urodeles (p. 289) is either, as in *Salamandra*, fused with the fenestra endonarina anterior into a fenestra endonarina communis (*fe. en*, figs. 16 A, 20) or else it forms a separate opening (*fe. enp*, fig. 46 B, C) in the lateral nasal wall, situated far from the fenestra endochoanalis (*fe. ench*, figs. 16 B, 17 B, 46 B, C) which is usually very large. In the majority of Urodeles the postero-ventral part of the lateral nasal wall is perforated by the fenestra lateralis nasi (p. 289; *fe. ln*, figs. 20, 46 C; cf. p. 411) which lies about as the fenestra endonarina posterior in *Porolepis*, though with the difference that it is generally situated somewhat further anteriorly and that both in *Salamandra* and most other Urodeles it is separated from the fenestra endochoanalis by a bridge of cartilage (lamina ectochoanalis). In the development and position of the openings here referred to there are thus fairly considerable differences between *Porolepis* and such Urodeles as *Salamandra*. In primitive Urodeles we find, however, conditions, which, as we shall now see, are more or less transitional between the conditions in the said two forms.

The fenestra endonarina posterior (*fe. enp*, fig. 40 A, C) in *Porolepis* has a posterior and larger part covered by dermal bones on the outside, and an anterior and fairly small part which is open and lies exactly medially to the fenestra exonarina posterior (*fe. exp*, fig. 41; *i. exp*, fig. 40 B) which it approximately equals in size. The anterior part, which consists principally of a notch, *i. enp*, in the anterior margin of the fenestra, was traversed by the posterior external nasal tube and is thus in fact the only part of the fenestra that is strictly comparable to the fenestra endonarina posterior in Urodeles. This part will therefore in the subsequent account be termed the fenestra endonarina posterior proper. The hinder part which is closed by dermal bones will be referred to as the large posterior part of the fenestra endonarina posterior.

The fenestra endonarina posterior proper as thus defined in *Porolepis* (*i. enp*, fig. 40 A, C) is a small opening in the lateral nasal wall. It lies antero-dorsally to the fenestra endochoanalis and postero-ventrally to the fenestra endonarina anterior (*fe. ena*); it is separated from the latter by a considerable part of the lateral nasal wall, more precisely the part of the lateral nasal wall that on its medial side bears the groove for the posterior external nasal tube (*gr. ntp*, fig. 46 A). The fenestra endonarina posterior in Urodeles (*fe. enp*, fig. 46 B, C) is also a small opening in the lateral nasal wall and has the same relations to the nasal capsule otherwise. It thus lies postero-ventrally to the fenestra endonarina anterior and is separated from that fenestra by part of the lateral nasal wall (often consisting principally of the nariodal bone) the medial side of which is provided with the internal nasolachrymal groove, that is the homologue of the groove for the posterior external nasal tube in *Porolepis* (*gr. ntp*, fig. 46 A). As pointed out above (p. 289), however, the fenestra in question in Urodeles has a somewhat varying position. In certain forms, such as *Plethodon* and *Spelerpes*, it lies in cartilage behind the nariodal bone far behind the fenestra endonarina anterior (fig. 46 B). In other forms with a nariodal bone it lies somewhat further forwards, at the posterior margin of that bone (fig. 46 C), whereas in forms without a nariodal, for instance *Salamandra*, it is fused with the fenestra endonarina anterior into a fenestra endonarina communis (*fe. en*, figs. 16 A, 20). As the Urodeles have in all probability arisen from *Porolepis* or closely related forms, the presence in *Plethodon* and *Spelerpes* of a separate fenestra endonarina posterior situated far posteriorly must be a primitive character. The conditions met with in such Urodeles as *Salamandra* must be assumed to have developed from a *Porolepis*-like form by a gradual migration of the fenestra endonarina posterior proper in a direction forwards and upwards towards the fenestra endonarina anterior, leading to a fusion of the two fenestrae. By such a migration the part of the lateral nasal wall primarily separating the fenestrae in question may gradually have been resorbed from behind forwards. Since the fenestra endonarina posterior as well as the fenestra endonarina communis in Urodeles is normally bounded by cartilage posteriorly, it may be assumed that the resorption as a rule proceeded simultaneously with a new formation of cartilage behind the migrating fenestra endonarina posterior proper. If this new formation of cartilage failed to take place, we might expect to find a narrow slit-like opening in the lateral nasal wall, an opening which would extend forwards and upwards from the large posterior part of the fenestra endonarina posterior and which would mark the distance that the fenestra endonarina posterior proper had moved forward. It is interesting to note that judging from reproductions given by Chung, a slit-like opening situated exactly as here outlined is actually found in certain primitive Urodeles. In *Hynobius leechii*, but most distinctly in *Pseudosalamandra* (Chung 1931, pl. 11, figs. 11, 12; pl. 12, figs. 15, 16), the postero-ventral part of the lateral nasal wall is perforated by an opening, the fenestra retronarina of Chung's descriptions, which, as will be shown below, is homologous to the large posterior part of the fenestra endonarina posterior in *Porolepis*. From that opening a narrow slit runs forward and upwards towards the fenestra endonarina posterior, from which it is separated by a bridge of cartilage. This bridge does not arise, however, until late in ontogeny and up to the metamorphosis the slit is therefore in communication with the fenestra endonarina posterior (Chung 1932).[1]

If the slit-like opening in the lateral nasal wall of the Hynobiids just dealt with actually arose in consequence of the forward migration of the fenestra endonarina posterior and thus marks the distance of this migration, we must of course expect that in larval stages it has something to do with the nasolachrymal duct, but as far as I can find such is not the case. This, as we shall now see, is due to modifications in the development of the posterior external nasal tube in connection with its transformation into a nasolachrymal duct.

In *Porolepis* the external opening of the posterior external nasal tube, that is to say the posterior external nostril, in all probability (cf. p. 407) lay immediately outside the fenestra exonarina posterior (*fe. exa*, fig. 41) and thus comparatively far antero-ventrally to the eye. On the other hand the posterior opening of the nasolachrymal duct in Urodeles[2], which is undoubtedly homologous to the posterior external nostril in *Porolepis*, lies at the anterior (medial) corner of the eye. We must assume, therefore, that during its transformation into a nasolachrymal duct the posterior external nasal tube was produced backwards as far as to the eye and that in connection with this development its posterior end shifted somewhat upwards. The nasolachrymal duct in very primitive Urodeles undoubtedly lay almost entirely in the internal nasolachrymal groove, and thus within the nasal cavity in a corresponding way as it did in *Porolepis* (in the groove *gr. ntp*, fig. 46 A). Owing to its lengthening backwards and probably also to a migration forwards of the fenestra endonarina posterior causing a shortening of the internal nasolachrymal groove, the nasolachrymal duct in modern Urodeles ultimately became to a large extent situated outside the nasal capsule along the lateral nasal wall. During its passage in the internal nasolachrymal groove and through the fenestra endonarina posterior the nasolachrymal duct in primitive recent Urodeles (see CHUNG 1931, pl. 11, figs. 1, 3, 5, 7, 9, 11; pl. 12, fig. 15; YATABE 1931, pl. 9, figs. 1, 2, 6—13, 16, 18, 20, 21) goes backward and downward towards the postero-ventro-lateral corner of the nasal capsule[1] and in these parts its course is thus quite similar to that of the posterior external nasal tube in *Porolepis.* Immediately after its exit from the fenestra endonarina posterior, however, it makes an abrupt bend upwards and then turns backwards towards the eye. On account of the abrupt upward bend just referred to it runs dorsally to the slit-like opening of the lateral nasal wall in *Hynobius leechii* and *Pseudosalamandra.* The fact that the nasolachrymal duct in primitive recent Urodeles makes a very peculiar upward bend and that the course of its anterior part is similar to that of the posterior external nasal tube in *Porolepis* strongly supports the opinion here advanced that the nasolachrymal duct of Urodeles is a transformed posterior external nasal tube which has gained connection with the eye.

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[1] In these forms the nariodal bone separates the fenestrae endonarinae anterior and posterior. As this bone does not develop until immediately before or during the metamorphosis, the slit in the lateral nasal wall in larvae in fact connects the "fenestra retronarina" also with the fenestra endonarina anterior.

[2] The nasolachrymal duct is provided with a single posterior opening in certain primitive Urodeles only. In the majority of the Urodeles it has two or more posterior openings, probably resulting from a subdivision of a single primary one (see Yatabe 1931; Watanabe 1936 a).

This opinion is further corroborated by the embryonic development of the nasolachrymal duct in Urodeles (I. W. WILDER 1925; YATABE 1931; SCHUCH 1934; WATANABE 1936 a). Despite the function of the nasolachrymal duct to carry secretion from the eye to the nasal sac, the part of it first to arise embryologically in Urodeles, according to WATANABE, is the anterior part nearest to the olfactory organ. The primordium is a solid strand of epithelium which quite early gains connection with the nasal sac. The transformation of this strand into a canal proceeds from the front backwards. The posterior opening of the canal thus formed lies at first in front of the eye on the exposed external face of the skin, but later on becomes folded into the anterior (medial) corner of the eye in connection with the formation of the eyelids (YATABE 1931, p. 293). In this connection it deserves to be mentioned that the nasolachrymal duct in *Xenopus* among the Anurans is said by PATERSON (1939 a, p. 402) to develop "during metamorphosis simply as an extension" of the wall of the nasal sac.

During its course backwards outside the nasal capsule the nasolachrymal duct in Urodeles lies in a groove, the external nasolachrymal groove, in the external face of the lateral nasal wall (p. 293). This groove, which lacks an equivalent in *Porolepis*, must obviously be a secondary formation which has arisen in Urodeles in connection with a change in position of the nasolachrymal duct in relation to the nasal capsule. As the crista rostro-caudalis is present and well developed even in *Porolepis*, it follows, of course, that the presence of this crista cannot possibly be caused by the external nasolachrymal groove. The current opinion that these two formations constitute together an initial stage towards the development of the turbinal foldings of higher Tetrapods is thus quite untenable (cf. p. 293).

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[1] In *Pseudosalamandra* the foremost part of the nasolachrymal duct lies in the straight anterior prolongation of the slit-like opening in the lateral nasal wall referred to above.

After its exit from the nasal capsule the posterior external nasal tube in *Porolepis* traversed the small fenestra exonarina posterior (see p. 372; *fe. exp*, fig. 41) situated in the exoskeleton between the lateral rostral and lachrymal bones. In *Holoptychius* and conceivably also in *Porolepis* the anterior margin of the lachrymal (*La*, fig. 33) has a pronounced notch in its anterior margin at the place where it enters the boundary of the fenestra exonarina posterior. The part of the external face of the lachrymal in *Holoptychius* surrounding this notch is comparatively strongly ornamented, a condition demonstrating beyond question that the posterior external tube in this form cannot have reached backwards from the fenestra endonarina posterior along the outside of the lachrymal. As there is no reason to assume that the posterior external nasal tube had a free external part, we must conclude that the posterior external nostril lay immediately externally to the fenestra exonarina posterior.

In primitive Urodeles, such as *Hynobius*, *Pseudosalamandra*, *Onychodactylus*, *Geomolge* and *Ranodon* (WIEDERSHEIM 1877, pl. 23, figs. 64, 69; CHUNG and YATABE 1931, pp. 264—265; pl. 8, figs. 1—7, 9; YATABE 1931, pl. 9, figs. 1, 6—12; CHUNG 1932, pp. 351—352), the part of the nasolachrymal duct situated outside the nasal capsule goes at first in the foremost part of the external nasolachrymal groove after which it enters and traverses a canal, the canalis nasolacrimalis (*c. dnl*, fig. 46 C), in a small dermal bone occupying the hinder part of the external nasolachrymal groove. This dermal bone, termed lachrymal by CHUNG and YATABE, lies on the outside of the hinder part of the lateral nasal wall and is pierced by the canalis nasolacrimalis in its anterior two thirds only. Behind the nasolachrymal canal the nasolachrymal duct continues backwards to the eye on the lateral side of the bone. In larval stages (*Hynobius*; CHUNG 1932) the bone in question is merely a thin lamina developed so as to form a groove, open outwards, for the nasolachrymal duct. During the further growth this groove is closed and transformed into the canalis nasolacrimalis.

The small bone in primitive recent Urodeles just dealt with may possibly represent the lachrymal of the *Porolepiformes* (*La*, figs. 33, 41, 46 A; cf. *Eusthenopteron*, p. 548; figs. 34, 55, 65 A, 68 A).[1] The last-mentioned bone is large in *Holoptychius* and was conceivably so also in *Porolepis*. It belongs to the palatoquadrate-cheek complex and is in the main situated laterally to the anterior ventral part of the orbit. Only a short anterior portion of it stretches forwards laterally to the posterior parts of the ethmoidal region, overlapping the area *od. La* and a dorsal portion of the area *od. La + Mx* of the ethmoidal shield (figs. 37, 40 B). This foremost portion has no contact with the ethmoidal region, being completely separated from it by the overlapped areas just referred to. It is this portion that enters the boundary of the fenestra exonarina posterior and which thus presents a notch for the posterior nasal tube in its anterior margin.

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[1] Whether, as maintained by GREGORY (1913, 1920; GREGORY and others 1935), the Crossopterygian lachrymal is the strict homologue of the lachrymal in mammals and should

If now the lachrymal in Urodeles is actually homologous to the similarly termed bone in *Porolepiformes* and has arisen from a lachrymal of the Porolepiform type, it must obviously be regarded as vestigial and highly modified. It may then be assumed to have arisen in about the following way: 1) Its sensory canal component and its entire orbital part became completely reduced. The reduction of these two parts may have been caused by the reduction of the anterior parts of the palatoquadrate (see pp. 412—413) and by the bone having lost its function as a protective organ of the infraorbital sensory canal. Only an anterior dorsal part of the bone would then persist, a part which would represent the portions in *Porolepiformes* that cover the area *od. La* and bear the notch forming the posterior boundary of the fenestra exonarina posterior. 2) The area of the ethmoidal shield overlapped by the bone (an area corresponding to the thin area *od. La* in *Porolepis*) became reduced. By the reduction of this area the persisting anterior part of the bone secondarily rested directly against the external face of the posterior part of the lateral nasal wall (as it does in primitive recent Urodeles). 3) In connection with the extension of the posterior external nasal tube backwards towards the eye and in consequence of the other modifications which have taken place in this tube during its transformation into a nasolachrymal duct, the notch in the anterior margin of the lachrymal forming the posterior boundary of the fenestra exonarina posterior was probably developed into a rostro-caudal groove (cf. fig. 46 B, *gr. dnl*) during a fairly early stage of the phyletic development of the Urodeles. This groove probably decreased in depth backwards and was also in other respects essentially as the groove for the nasolachrymal duct in the lachrymal in larvae of *Hynobius*. In later phyletic stages it was

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thus definitely be termed lachrymal is a question that cannot be discussed in this work (cf. GAUPP 1910; SALOMON 1930; SÄVE-SÖDERBERGH 1935, pp. 119—120; STADTMÜLLER 1936, pp. 627—628).

grown over by bone and transformed into a canalis nasolacrimalis in a corresponding way as in later embryonic stages in *Hynobius*.

Besides the lachrymal there is, in the primitive recent Urodeles enumerated above (p. 407), another dermal bone, the so-called prefrontal (*Pfr*, fig. 46 B; CHUNG and YATABE 1931). In view of its position this bone may possibly represent the posterior tectal in *Porolepiformes* (*Te. p*, fig. 33). In the majority of Urodeles the lachrymal seems to have disappeared completely whereas the "prefrontal" is still present immediately in front of the orbit. In the Urodeles devoid of a lachrymal the nasolachrymal duct traverses, as in *Triturus* (ERDMANN 1933, p. 576), *Diemictylus* (CHUNG and YATABE 1931, pp. 260—261), *Oedipus* and others (NOBLE 1921, p. 3; pl. 2, fig. 2), an opening in the suture between the maxillary and the "prefrontal", but may also, as in *Salamandra*, be secondarily enclosed in the latter bone.[1]

As shown above the nasolachrymal duct has thus during the phyletic development of the Urodeles undergone considerable changes as regards its position. In connection with the forward migration of the fenestra endonarina posterior the anterior part of the duct has partly shifted outwards through the lateral nasal wall. The posterior part of the duct has sunk deeper inwards and has thus secondarily become enclosed in the lachrymal. In the advanced forms in which the lachrymal is reduced this part of the duct has become enclosed secondarily in the underlying part of the "prefrontal" or in the suture between this bone and the maxillary.

The anterior part of the fenestra endonarina posterior in *Porolepis* which constitutes the fenestra endonarina posterior proper, has been discussed above. We shall now proceed to the large posterior part of the fenestra endonarina posterior in *Porolepis* and in this connection we shall also deal with the fenestra endochoanalis in this form. As regards these formations, *Porolepis* will first be compared to *Salamandra*.

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[1] According to STADTMÜLLER (1936, p. 627) the part of the "prefrontal" pierced by the nasolachrymal duct represents the lachrymal which is thus not reduced. The following seems, however, to contradict this opinion and to support instead the opinion here advanced that the nasolachrymal duct is secondarily enclosed in the "prefrontal" (cf. NOBLE 1921, pp. 3—4): a) No independent lachrymal has been observed in larval stages either of *Salamandra* or of other forms in which this bone is absent in adults; b) as we have seen, the lachrymal has in all probability undergone a considerable reduction during the phyletic development of the Urodeles and obviously tends to disappear completely. In such forms as *Triturus*, *Diemictylus* and *Oedipus* it is certainly completely reduced; c) in the Urodeles in which the lachrymal is developed as an independent bone the part of it enclosing the nasolachrymal duct overlaps the ventro-lateral corner of the "prefrontal" (see CHUNG and YATABE 1931). If the lachrymal of these forms were reduced the nasolachrymal duct would cross the ventro-lateral corner of the "prefrontal" on the outside, which it actually does in larvae of *Salamandra* (STADTMÜLLER 1924, p. 206) and *Siredon* (GROTE 1926, figs. 4—6); d) the nasolachrymal duct is not enclosed in the "prefrontal" until late during the embryonic development (NOBLE 1921; STADTMÜLLER 1924).

The large posterior part of the fenestra endonarina posterior in *Porolepis* (*fe. enp*, fig. 40 A, C) is situated in the postero-ventral part of the lateral nasal wall and in the main behind Seydel's palatal process. It is continuous ventrally with the fenestra endochoanalis (*fe. ench*) and forms together with this and with the fenestra endonarina posterior proper the fenestra ventro-lateralis (pp. 370—371; *fe. vl*). Laterally it is closed throughout by dermal bones, its upper part by the ventral corner of the portion of the ethmoidal shield that is overlapped by the lachrymal (*od. La*), its ventral part by the lachrymal and the maxillary. The fenestra endochoanalis is relatively small and perforates the postero-lateral part of the solum nasi that lies in the main behind Seydel's palatal process. In *Salamandra* (figs. 16, 20) we find also an opening in the postero-ventral part of the lateral nasal wall. This opening, the fenestra lateralis nasi (p. 289; *fe. ln*), is separated, however, from the fenestra endochoanalis by that part of the solum nasi and the lateral nasal wall, the lamina ectochoanalis (*la. ech*), from which Seydel's palatal process projects backwards, and it thus lies somewhat further forwards than the large posterior part of the fenestra endonarina posterior in *Porolepis*. It is occupied by a lateral bulge of the nasal sac. The fenestra endochoanalis is considerably larger than in *Porolepis* and lies throughout in front of Seydel's palatal process. The choana is situated further medially in *Salamandra* than it was in *Porolepis*, judging from the position of the fenestra endochoanalis.

Turning to primitive Urodeles and larvae of Urodeles we find the following conditions. In older larvae of *Ambystoma* (HIGGINS 1920, pp. 10—14, pl. 1, figs. 5—8) the fenestra endochoanalis is, quite as in *Porolepis*, a small opening in the postero-lateral part of the solum nasi. During the subsequent larval development this opening widens through resorption, so that the fenestra endochoanalis in adults (fig. 17 B) is of a corresponding size as in *Salamandra* (fig. 16 B). In Hynobiids (CHUNG and YATABE 1931; CHUNG 1931) the fenestra endochoanalis is large, but the choana lies underneath the postero-lateral corner of the nasal cavity and has, at least in certain forms (CHUNG 1931, pl. 12, fig. 18), a position postero-medially to Seydel's palatal process corresponding exactly to the position it must have had in *Porolepis*. It is particularly interesting that in certain Hynobiids, viz. *Hynobius leechii*, *H. tsushimensis* and *Pseudosalamandra* (CHUNG 1931, p. 379), the fenestra endochoanalis is continuous laterally with an opening in the postero-ventral corner of the lateral nasal wall. This opening (fenestra retronarina, CHUNG) is closed laterally by dermal bones, and as both in this and other respects it agrees essentially with the large posterior part of the fenestra endonarina posterior in *Porolepis*, it is conceivably a homologue of that part. Together with the fenestra endochoanalis it forms an opening corresponding to the fenestra ventro-lateralis in *Porolepis*. As pointed out above (pp. 404—405), it is continued by an oblique slit-like opening in the lateral nasal wall, an opening which up to the metamorphosis is connected with the fenestrae endonarinae anterior and posterior. In larvae of these forms the postero-lateral part of the nasal capsule thus has a large opening including the fenestra endochoanalis. The presence of this large opening in larvae of primitive Urodeles is of particular interest as there is most probably a similar opening in *Holoptychius*, the geologically youngest genus of the *Porolepiformes*.

In certain *Hynobius* species (*H. retardatus, H. naevius*) and in *Onychodactylus* (Chung 1931) the fenestra endochoanalis is separated from the opening in the lateral nasal wall by a bridge of cartilage which, as far as may be judged at present, is a secondary formation due to progressive development of cartilage. In *Hynobius nebulosus* and *Geomolge* this progressive development of cartilage has proceeded still further, so that the opening in the postero-ventral part of the lateral nasal wall has become completely closed (cf. p. 289).

The opening in question in the lateral nasal wall in Hynobiids was termed by Chung (1931) the fenestra retronarina (infraconchalis). Chung thus seems to regard it as a homologue of the fenestra lateralis (infraconchalis) nasi in advanced Urodeles such as *Salamandra*. I am not fully convinced, however, that such an interpretation is correct. The opening now discussed in Hynobiids is closed by a membrane which may in exceptional cases be pierced by a fine nerve-branch (Chung 1931, p. 387). The fenestra lateralis nasi in *Salamandra*, on the other hand, is developed for a lateral bulge of the nasal sac and also lies somewhat further forwards than the "fenestra retronarina" in primitive Urodeles and the large posterior part of the fenestra endonarina posterior in *Porolepis* (cf. p. 410). In view of these conditions and on account of the absence of an opening in the posterior part of the lateral nasal wall in certain Hynobiids (*Hynobius nebulosus*, *Geomolge*) it is not impossible that the fenestra lateralis nasi (*fe. ln*, fig. 46 C) in higher Urodeles is a new formation caused by the lateral bulge of the nasal sac.

As we have seen (p. 289), the tectum nasi and the adjacent parts of the anterior and medial nasal walls are completely developed in older larvae of Urodeles, and are pierced only by several foramina for twigs of the medial terminal profundus branch and vessels. These foramina (*f. 5a. Ma*, *f. 5a. Md*, figs. 16, 17 A, 46 C) agree well in position with the canals (*c. prt*, figs. 39, 42 A, C, E, 43, 46 A) in the corresponding parts of the nasal walls in *Porolepis* and are certainly equivalent to them. During the last part of the larval development of the Urodeles a large opening, the fenestra dorsalis nasi (p. 289; *fe. dn*, figs. 16, 17, 46 C), arises through resorption in the tectum nasi. This opening has no homologue in *Porolepis*, and, as is obvious from its embryonic development, it must be a secondary formation that has arisen within the Urodele group.

The fact that the fenestra endonarina anterior (*fe. ena*) is larger in Urodeles (fig. 46 B, C) than in *Porolepis* (fig. 46 A) is certainly due simply to the regressive development of the ethmoidal region that must have taken place during the phyletic development of the Urodeles.

The palatoquadrate in *Porolepis* and *Holoptychius* is still imperfectly known, but this much is fully clear that its anterior part was strongly developed (p. 357). The pars autopalatina was broad and plate-like and probably formed a complete floor of the foremost part of the orbit quite as in *Eusthenopteron* (figs. 54, 55). The presence in *Porolepis* of two articular fossae, the fossa *art. aup?* and the autopalatine fossa (*fo. aup*, fig. 37; cf. pp. 386—387), situated at the ventro-lateral and the ventro-medial corners of the postnasal wall, the latter also extending onto the adjacent part of the interorbital wall, renders it likely that the palatoquadrate was provided anteriorly with two short, rounded articular processes, an antero-lateral one which articulated against the fossa *art. aup?*, and an antero-medial one, which fitted into the autopalatine fossa. The position of these two processes would be such that they must be regarded as homologues of the antero-lateral and antero-medial processes of the palatoquadrate in Urodeles (pp. 296—300). As the articular fossae in *Porolepis* are both lined with a periostal bone layer, it is obvious that there was no fusion between the palatoquadrate and the endocranium at these places (cf. p. 457—458). The fusion that takes place in Urodeles between the antero-medial and antero-lateral processes and the endocranium must therefore be secondary and must have arisen in the Urodele group, an opinion which is corroborated by the embryological conditions. *Porolepis* differs from Urodeles also in that the anterior part of its palatoquadrate is much more strongly developed. It is therefore interesting to find that among the Urodeles the anterior part of the palatoquadrate is most strongly developed in the Hynobiids (particularly *Ranodon*), which, as we have seen, also in other respects have retained several primitive features in the snout and which are to a certain extent transitional between *Porolepis* on the one hand and advanced Urodeles, such as *Salamandra*, on the other. In advanced Urodeles the anterior part of the palatoquadrate does not develop beyond the procartilaginous stage and in adults it does not extend forwards to the ethmoidal region. It is thus obvious that the anterior part of the palatoquadrate in Urodeles has undergone a regressive development. In this connection it should be especially stressed that the reduction of the foremost part of the palatoquadrate cannot possibly have caused the special very characteristic type of nerve and vascular supply of the snout found in Urodeles, for we have seen that this type of nerve and vascular supply was fully differentiated already in the lower Devonian *Porolepis* among the *Porolepiformes* (cf. p. 308).

The presence in *Porolepis* and *Holoptychius* of a well developed basipterygoid process (*br. bp*, fig. 44; pl. 3, figs. 1, 2; pl. 4; pl. 5, fig. 2) and in *Holoptychius* also of an antotic process (*pr. aot*, fig. 44) on the endocranium[1] shows that the palatoquadrate in *Porolepiformes* was probably provided with both a processus basalis and a processus ascendens quite as in Urodeles (STADTMÜLLER 1936, pp. 575, 581—582; DE BEER 1937, pp. 419—420).

Finally, a brief comparison will now be made between the dermal bones of the snout in *Porolepiformes* and those in Urodeles.

As has already been pointed out (p. 399), the "premaxillary" has much the same shape and position in *Porolepiformes* and Urodeles. In both the groups it consists morphologically of three parts, pars dentalis (Pmx_1, figs. 16 B, D, 46; pl. 3, fig. 3; cf. *pmxt*, figs. 36 A, 37 A, 40 B; processus dentalis, HERTWIG 1874; Alveolarfortsatz, WIEDERSHEIM 1877), pars facialis (Pmx_2, figs. 16 A, D, 18 B, 46 B, C; cf. fig. 33; processus nasalis, HERTWIG 1874; processus ascendens, WIEDERSHEIM 1877; processus prenasalis, GAUPP 1905) and pars palatina (Pmx_3, figs. 16 B, D, 46; pl. 3, fig. 3; cf. fig. 36 A, *la. pal*; processus palatinus, HERTWIG 1874). The first-mentioned part forms the tooth-bearing margin of the bone, whereas the pars facialis and pars palatina either cover the antero-lateral part of the outer face and the antero-lateral part of the ventral face of the divisio prenasalis communis (*Porolepiformes*) or participate to a large extent in the boundary of the cavum prenasale secondarily widened through the partial resorption of the divisio prenasalis communis (Urodeles). Its practically complete agreement as to shape and position shows that the "premaxillary" must be homologous in the two groups. As the "premaxillary" in *Porolepiformes* certainly is a complex bone, a naso-premaxillary, or, more probably still, a naso-rostro-premaxillary, we must assume that this applies also to the "premaxillary" of Urodeles (cf. p. 498).

In this connection the circumstance is of importance that the pars facialis of the "premaxillary" in Urodeles is fairly variable in its development. In certain Urodeles, above all in the primitive families *Hynobiidae* and *Cryptobranchidae* (OKAJIMA 1908, pl. 13, fig. 1; DUNN 1923, p. 447; CHUNG and YATABE 1931, pl. 8) this part of the bone is short. In several of these forms it is also low and broad, as in *Porolepiformes*. In other forms, e. g. *Ambystoma* (fig. 18 B; WIEDERSHEIM 1877, pl. 23, fig. 76; 1879, pl. 11, fig. 6) and *Salamandra* (fig. 16 A, D), it is very long in a rostro-caudal direction, to a considerable extent overlapping the so-called frontal, which must be due to a secondary lengthening. The pars facialis has thus undergone a progressive development in Urodeles (cf. I. W. WILDER 1924).

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[1] The antotic process has hitherto been found in *Holoptychius* only. Judging from its position this process must correspond to the similarly termed process in Coelacanthids (STENSIÖ 1932, pp. 30—32; figs. 8, 12—14; HOLMGREN and STENSIÖ 1936, pp. 348—350, 354; figs. 266, 267; SÄVE-SÖDERBERGH 1936, pp. 145—147).

The maxillary (*Mx*) in Urodeles (see for instance WIEDERSHEIM 1877; CHUNG and YATABE 1931) also consists of three parts, pars dentalis, pars facialis, and pars palatina (Mx_1, Mx_2, Mx_3, figs. 16 A, B, D, 18, 46 B, C). The maxillary in *Porolepiformes* consists chiefly of a pars dentalis (*Mx*, figs. 33, 41; Mx_1, fig. 46 A). The pars facialis is weakly developed in them and no pars palatina appears to be present.

As has been shown (pp. 407—408), the lachrymal (*La*) in Urodeles (fig. 46 B, C) has become strongly or entirely reduced. A homologue of the antero-dorsal part of the lachrymal in *Porolepiformes* (figs. 33, 41, 46 A) persists in primitive Urodeles, whereas the bone has become completely reduced in higher Urodeles.

As far as we know no bone corresponding to the lateral rostral (*R. l*, figs. 33, 46 A) in *Porolepiformes* exists in Urodeles. This bone seems to have disappeared completely.

The relatively few dermal bones present on the medial dorsal parts of the snout in Urodeles show a fairly varying development and disposition and overlap each other to a considerable extent (see figs. 16 A, D, 18, 46 B, C; WIEDERSHEIM 1875; 1877; 1879; W. K. PARKER 1877; 1882 a; 1882 b; OKAJIMA 1908; NOBLE 1921; GROTE 1926; AOYAMA 1927; 1930; BOLKAY 1928; CHUNG and YATABE 1931; HERRE 1933; 1935; 1939; STADTMÜLLER 1936). It does not seem very likely that variations in the size and number of these bones are due to varying fusions of bones or bone components found in *Porolepiformes* (pp. 346—352; figs. 33, 46 A). It is much more conceivable that only certain of the bones present in *Porolepiformes* persist and that the other ones have disappeared. The variations would then be due simply to progressive or regressive developments of the persisting bones (cf. NOBLE 1921).

A comparison between the dermal bones now considered on the dorsal medial parts of the snout in Urodeles with the correspondingly situated bones in *Porolepiformes* is at present very difficult. An attempt at an interpretation of these bones will, however, be made here, but this attempt is provisional only and is subject to strong reservations.

As has been mentioned above the "prefrontal" in Urodeles (*Pfr*, figs. 16 A, D, 18 C, 46 B, C) probably represents the posterior tectal of the *Porolepiformes* (*Te. p*, fig. 33). The "nasal" in Urodeles (*Na*, figs. 16 A, D, 18 B; "*Na*" fig. 46 B, C) may correspond to one of the hinder anterior tectals in *Porolepiformes* (*Te. a*, figs. 33, 46 A). The "prenasal" described by ERDMANN (1933, p. 576, fig. 7; cf. DE BEER 1937, p. 185) in *Triturus* may perhaps be an equivalent to one of the foremost anterior tectals in *Porolepiformes*. The so-called frontal in Urodeles (*Fr*, figs. 16 A, D, 18 C; "*Fr*", fig. 46 B, C), which lies on the foremost part of the orbitotemporal region and an adjacent part of the ethmoidal region, can hardly be strictly homologous to the frontal in *Porolepiformes* (*Fr*, fig. 33) which lies above the posterior part of the orbitotemporal region (cf. p. 344 above). It is difficult to decide to which of the bones in *Porolepiformes* it is nearest comparable. Judging from its position in larval stages (fig. 16 D; see WINTREBERT 1922, fig. 28; STADTMÜLLER 1924, p. 204; AOYAMA 1930, p. 169; ERDMANN 1933, p. 574, fig. 6; OKUTOMI 1936, p. 33), it most likely corresponds to the hindmost nasal of the *Porolepiformes* (fig. 33; cf. WESTOLL 1938 a, b; 1940), but it may also be a postrostral.

The parasphenoid (*Psph*) is broad both in *Porolepiformes* (figs. 37, 44; pl. 4, fig. 1; pl. 5, fig. 2) and Urodeles (fig. 16 B) and in neither group does it go further forward than about to the transition between the ethmoidal and orbitotemporal regions. In *Porolepis* it is provided with a median tooth-bearing ridge which is absent in *Holoptychius* and Urodeles.

The vomer in *Porolepiformes* (*Vo*, figs. 37 A, 44, 46 A; pl. 5, fig. 2) agrees well in shape and position with the vomer in certain Urodeles, e. g. *Onychodactylus* (OKAJIMA 1908, pl. 13, fig. 2) and *Ambystoma* (WIEDERSHEIM 1875, pl. 13, fig. 103, "*Triton*" *ensatus*; 1877, pl. 23, fig. 77; 1879, pl. 11, fig. 8). As in those Urodeles it is thus on the whole a quadrilateral and almost rectangular bone which lies antero-laterally to the anterior end of the parasphenoid and which from its sutural connection with the latter bone extends in an antero-lateral direction to the pars palatina of the "premaxillary" of its side. At the very anterior tip of the parasphenoid it reaches or at any rate closely approaches the median line. Between the vomers of either side and bounded by them postero-laterally and by the partes palatinae of the "premaxillaries" anteriorly and antero-laterally there is a large median opening in the dermal skeleton of the palate. This opening, the anterior palatal fenestra, which is well developed also in *Salamandra* (fig. 16 B), is situated underneath the cavum internasale and cavum prenasale.

However, the vomer displays considerable variations as to its development in various Urodele forms (see inter alia WIEDERSHEIM 1875;

1877; 1879; W. K. PARKER 1877; 1882 a; 1882 b; BOLKAY 1928), some of which will now be briefly commented upon.

In several Urodeles, such as *Cryptobranchus* (ANTON 1908, pl. 10, fig. 5), *Spelerpes*, *Triturus*, *Plethodon* and *Salamandrina* (WIEDERSHEIM 1877, pl. 21, fig. 48; pl. 26, figs. 118—122, 129; pl. 27, fig. 134), the vomer is provided with an ascending lamina (Vo_a, fig. 46 B, C) which lies within the cavum internasale, lining its lateral wall. It is indeed interesting that a very similar ascending vomeral lamina occurs also in *Holoptychius* (figs. 44, 46 A). In several Urodeles, e. g. the majority of Hynobiids (fig. 18 A), *Ambystoma* (fig. 18 B) and *Salamandra* (fig. 16 B), the internasal and prenasal cavities are completely devoid of a floor of dermal bones. In other Urodeles they have such a floor, more or less complete, formed by the vomers of both sides which extend towards one another and may even meet in a long median suture. They do so for instance in *Triturus* (WIEDERSHEIM 1877, pl. 25, fig. 111; pl. 27, figs. 136, 141) in which the anterior palatal fenestra is represented by a small median opening only, situated in the suture between the vomers. As the internasal and prenasal cavities are wide open ventrally both in *Porolepiformes* and primitive Urodeles, the presence of a floor of dermal bones underneath them in many Urodeles must obviously be due to a secondary progressive development of the vomers. In several Urodeles, inter alia *Salamandra* (fig. 16 B), the vomer is provided with a strong posterior tooth-bearing process, which covers the parasphenoid from below. This process is regarded by several writers (see STADTMÜLLER 1936, pp. 638—639; DE BEER 1937, pp. 184—185) as a dermopalatine secondarily fused with the vomer, forming with this a vomero-palatine. As is well known, the dermopalatine is, however, a dermal bone belonging to the palatoquadrate and, as pointed out above (p. 300), it has in all probability disappeared completely in Urodeles in connection with the reduction of the anterior part of the palatoquadrate. WINTREBERT (1922; cf. AOYAMA 1930, pp. 173—175), who has strongly maintained that there is no compound vomeropalatine in Urodeles, regards the posterior tooth-bearing process of the vomer in Urodeles simply as part of the vomer itself, formed by a progressive development of the bone in a posterior direction. It is not impossible that this may be true, but another explanation of the origin of the process in question must also be taken into account. In certain Crossopterygians we find behind the vomer, in a position corresponding to that of the posterior tooth-bearing process in Urodeles, a tooth-bearing plate which is more or less strongly fused with the parasphenoid. This tooth-plate is paired in certain Coelacanthids (fig. 81). Whether it was present also in *Porolepiformes* cannot be decided with certainty, but judging from the appearance of the lower face of the parasphenoid, this was very likely the case, and if so it is paired in *Porolepis.*[1] A correspondingly situated paired tooth-bearing plate occurs in certain Urodeles, viz. in Plethodontids (Wiedersheim 1877, pl. 23, fig. 74; pl. 25, figs. 95, 99, 103, 106; Dunn 1917, figs. 2, 6, 10), in which the vomer is devoid of a posterior tooth-bearing process. The conditions in Plethodontids thus seem to indicate that the posterior tooth-bearing process of the vomer in several Urodeles, inter alia *Salamandra*, corresponds to the paired tooth-bearing plate, the parasphenoid dental plate, in Crossopterygians. The opinion that the posterior process of the vomer now discussed is the equivalent of the tooth-bearing paired plate in Plethodontids has previously been advanced by Mrs. I. W. Wilder (1920, p. 349; cf. Dunn 1922, p. 423; Noble 1931, p. 477). She is of opinion, however, that this plate has become secondarily detached from the vomer, which, judging from the presence of an independent paired parasphenoid dental plate in Crossopterygians, is hardly plausible.

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As may be gathered from the above comparison between Porolepiform Crossopterygians and Urodeles, they display some very remarkable points of agreement in the development of the snout. They may be summarized as follows.

1) The internasal wall is broad and does not form any nasal septum. It lodges the ethmoidal part of the cranial cavity and in front of that a large cavum internasale which opens ventrally.

2) The divisio prenasalis communis is short and broad. It lodges a cavum prenasale which opens ventrally and forms an anterior continuation of the cavum internasale.

3) The internasal and prenasal cavities in Urodeles are developed for the intermaxillary gland and must in all probability have housed such a gland also in the *Porolepiformes.*

4) The nasal cavity lies in the lateral part of the ethmoidal region far apart from that of the opposite side (cf. No. 1).

5) The walls of the nasal cavity are fairly complete both in *Porolepiformes* and older larvae of Urodeles. (The fenestra dorsalis nasi in Urodeles is a secondary formation which arises during the metamorphosis).

6) The fenestra endonarina posterior in *Porolepis* consists of two parts, a small anterior one, the fenestra endonarina posterior proper, homologous to the fenestra endonarina posterior of primitive Urodeles,

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[1] This is clearly shown by the presence of the tooth-bearing median ridge developed on the parasphenoid.

and a large posterior one which is the strict equivalent of the fenestra "retronarina" in primitive Urodeles. The latter opening in *Porolepis* and primitive Urodeles is situated in the postero-ventral corner of the lateral nasal wall and is continuous ventrally with the fenestra endochoanalis.

7) The fenestra endochoanalis is in *Porolepis*, as in older larvae of certain Urodeles, a relatively small opening in the postero-lateral part of the solum nasi.

8) In *Holoptychius* the fenestrae endonarinae anterior and posterior and the fenestra endochoanalis form together a continuous opening in the same way as in older larvae of Urodeles.

9) The tectum nasi and the adjacent parts of the prenasal and medial nasal walls are pierced by a large number of fine canals or foramina for the twigs of the medial terminal profundus branch, and for vessels.

10) The postnasal wall is pierced by a wide medial and one or more finer lateral profundus canals or foramina.

11) There is a Seydel's palatal process, separated from the postero-ventral part of the lateral nasal wall by an incisura ectochoanalis.

12) The nasal cavity consists of a main chamber and a lateral recess only. Its anterior and antero-lateral parts are thus not subdivided into compartments, and no medial recess is developed.

13) The lateral recess occupies the postero-ventro-lateral part of the nasal cavity and is in open communication anteriorly and medially with the main chamber and posteriorly with the mouth cavity. It is bounded ventrally by the postero-lateral part of the solum nasi, laterally and dorso-laterally by the postero-ventral part of the lateral nasal wall, and dorsally by the crista rostro-caudalis, which protrudes medially into the nasal cavity from the lateral nasal wall.

14) Immediately dorsally to the crista rostro-caudalis there is a groove running rostro-caudally on the inside of the lateral nasal wall. This groove goes from close behind the fenestra endonarina anterior backwards to the fenestra endonarina posterior. In Urodeles it lodges the nasolachrymal duct; in *Porolepis* it was developed for the posterior external nasal tube, which is the homologue of the nasolachrymal duct. (The part of the lateral nasal wall bearing the groove has retained its bony tissue in primitive Urodeles and forms the nariodal bone).

15) The various points of agreement in the nasal cavity show that the nasal sac in *Porolepiformes* must on the whole have been similarly developed as the one in Urodeles. In *Porolepiformes* the nasal sac must thus have consisted of a main part and a lateral diverticle. The main part opened outwards through two nasal tubes, one anterior external, and one internal (choanal). The lateral diverticle consisted of a dorsal

(anterior) division situated above the crista rostro-caudalis, and a ventral (posterior) division lying in the lateral recess. The dorsal division was continued backwards by a posterior external nasal tube homologous to the nasolachrymal duct in Urodeles. Its ventral division, which probably corresponded to the so-called Jacobson organ in Urodeles, formed a sinus lateralis nasi, which opened backwards into the mouth cavity through a sulcus maxillo-palatinus. This sulcus was bounded ventrally by a plica palatina supported by Seydel's palatal process.

16) The forebrain in *Porolepiformes* was conceivably on the whole as that in Urodeles. The bulbus olfactorius lay ventro-laterally to the hemisphere of its side.

17) The lateral parts of the snout were in *Porolepiformes* supplied by the n. profundus in a similar way as in Urodeles. As in Urodeles the r. maxillaris V was weakly developed and apparently hardly reached into the snout.

18) The vascular system of the snout in *Porolepiformes* was certainly very similar to that in Urodeles. The lateral parts of the snout both received their blood and were drained by vessels which left and emerged into the medial part of the orbit. No vessels of any importance passed from or to the orbit laterally to the fenestra endochoanalis.

19) The n. profundus in *Porolepiformes* was strongly developed, as in Urodeles, and also branched as the corresponding nerve in Urodeles.

20) Also the other nerves of the snout in *Porolepiformes* seem on the whole to have resembled the corresponding nerves in Urodeles.

21) The palatoquadrate in *Porolepiformes* is provided with an antero-medial and probably also with an antero-lateral articular process. The antero-medial process, which is connected with the endocranium at the corner between the postnasal and interorbital walls, corresponds to the similarly situated process in larvae of several Urodeles. The antero-lateral process, which articulates against the postero-ventral corner of the postnasal wall, is certainly the equivalent of the similarly termed process in the adult *Ranodon.* In addition, the palatoquadrate in *Porolepiformes*, as that in Urodeles, has both a processus basalis and a processus ascendens.

22) The "premaxillary" has a similar shape and position and is in both groups a complex bone, a rostro-premaxillary or naso-rostro-premaxillary.

23) The parasphenoid is broad and hardly goes forwards underneath the ethmoidal region.

24) The vomer in *Porolepiformes* agrees in development and position with the vomer in primitive Urodeles. In *Holoptychius*, as in certain Urodeles, it is provided with an ascending lamina, which covers the lateral wall of the cavum internasale.

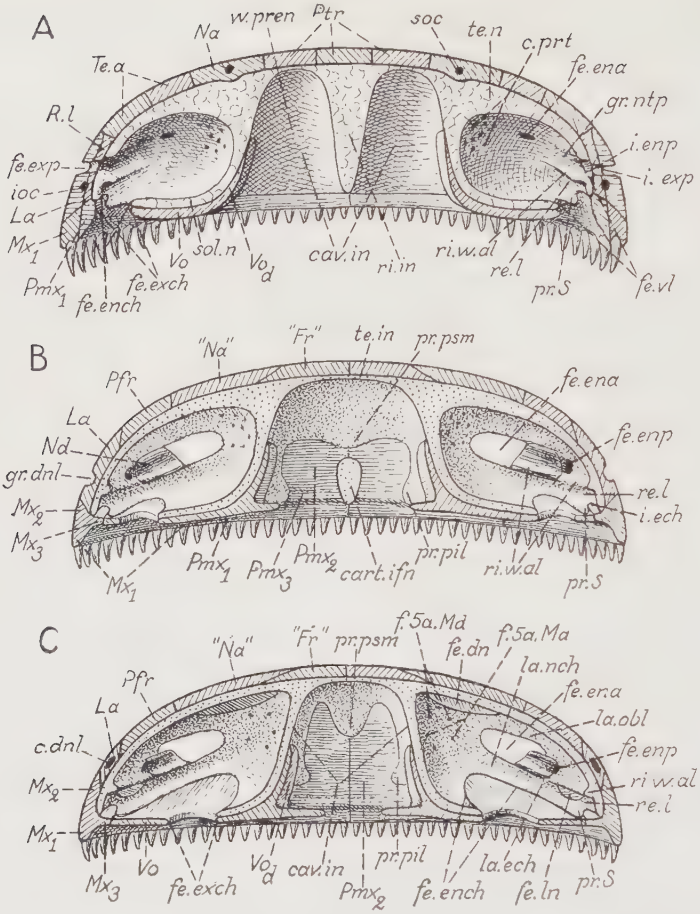
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Fig. 46. Three somewhat diagrammatic drawings illustrating the probable development of the snout in Urodeles from one of a *Porolepis*-like type. All the figures show the snout from behind with the hindmost part including the postnasal wall removed. Cross-sections through endocranial bony tissue reticulated, through dermal bones ruled. Cartilage dotted. *A*, *Porolepis spitsbergensis* but with the sutures of the ethmoidal shield and the ascending lamina of the vomer approximately after *Holoptychius*. *B*, primitive Urodele stage. *C*, more advanced Urodele stage.

"Fr", Urodele frontal, probably homologous to the most posterior nasal or to some of the postrostrals, but certainly not to the frontal of the *Porolepiformes*; *La*, lachrymal; Mx_1, Mx_2, Mx_3, pars dentalis, pars facialis, and pars palatina of maxillary; *Na*, nasal; *"Na"*, Urodele nasal, probably homologous to one of the anterior tectals in *Porolepiformes*; *Nd*, nariodal; Pmx_1, Pmx_2, Pmx_3, pars dentalis, pars facialis and pars palatina of "premaxillary" (rostro-premaxillary or naso-rostro-premaxillary); *Pfr*, "prefrontal", probably homologous to the hindmost tectal in *Porolepiformes*; *Ptr*, postrostrals; *R. l*, lateral rostral; *Te. a*, anterior tectal; *Vo*, vomer; Vo_d, ascending lamina of vomer; *cart. ifn*, cartilago infranasalis (in section), probably a vestige of the internasal ridge in *Porolepiformes*; *cav. in*, cavum internasale; *c. dnl*, canalis nasolacrimalis; *c. prt*, canals for twigs of medial terminal profundus branch; *fe. dn*, fenestra dorsalis nasi; *fe. ena*, fenestra endonarina anterior; *fe. ench*, fenestra endochoanalis; *fe. enp*, fenestra endonarina posterior; *fe. exch*, fenestra exochoanalis; *fe. exp*, fenestra exonarina posterior; *fe. ln*, fenestra lateralis nasi; *fe. vl*, fenestra ventro-lateralis; *f. 5a. Ma*, *f. 5a. Md*, foramina for

25) Ventrally to the internasal and prenasal cavities there is in *Porolepiformes* and several Urodeles a large opening in the dermal skeleton of the palate, the anterior palatal fenestra, which is bounded postero-laterally by the vomers and antero-laterally by the partes palatinae of the "premaxillaries".

As shown above, there are also many important differences between *Porolepis* and such a Urodele as for instance *Salamandra*. The ethmoidal region in *Porolepis* is very completely developed and ossified throughout, whereas the corresponding region in *Salamandra* is much more incomplete and built up of cartilage only. The same applies to the development of the orbitotemporal region and the anterior parts of the palatoquadrate in these forms. We have seen, however, that the differences between *Porolepis* and primitive Urodeles are in several respects much smaller than between *Porolepis* and *Salamandra*. It is of particular interest, too, that in many characters *Porolepis* agrees much more closely with older larvae of Urodeles than with adult Urodeles. During their oldest larval stages and above all during the metamorphosis the Urodeles undergo great changes in the structure of the ethmoidal region. These changes, among which may be mentioned the resorption of certain skeletal parts, the increase in size of the nasal cavities at the cost of the breadth of the internasal wall, and the withdrawal of the brain to the orbitotemporal region, to a certain extent reflect the way in which the phyletic development must be assumed to have taken place from Porolepiform-like ancestors to such a highly specialized Urodele as *Salamandra*.

With regard to the dermal bones of the dorsal side of the snout *Porolepiformes* and Urodeles differ considerably from each other. It is obvious, however, that the differences in this respect are smaller between *Porolepiformes* and primitive Urodeles than between *Porolepiformes* and more advanced Urodeles such as *Salamandra*. It is also readily seen that the bones in question in Urodeles must be greatly modified and that they cannot represent but a few of the bones which enter into the formation of the dorsal parts of an ethmoidal shield of a Porolepiform type. If some of the dermal bones in an ethmoidal shield of a Porolepi-

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anterior and dorsal twigs of medial terminal profundus branch, corresponding to canals *c.prt* in *Porolepiformes*; *gr.dnl*, groove for ductus nasolacrimalis; *gr.ntp*, groove for posterior external nasal tube; *i.ech*, incisura ectochoanalis; *i.enp*, notch in margin of fenestra ventro-lateralis for posterior external nasal tube (this notch constitutes the main part of the fenestra endonarina posterior proper); *i.exp*, notch in margin of ethmoidal shield for posterior nasal tube; *ioc*, infraorbital sensory canal; *la.ech*, lamina ectochoanalis; *la.nch*, lamina nariochoanalis; *la.obl*, lamina obliqua; *pr.pil*, processus prenasalis inferior lateralis; *pr.psm*, processus prenasalis superior medius; *pr.S*, Seydel's palatal process; *re.l*, lateral recess of nasal cavity; *ri.in*, internasal ridge; *ri.w.al*, crista rostrocaudalis; *soc*, supraorbital sensory canal; *sol.n*, solum nasi; *te.in*, tectum internasale; *te.n*, tectum nasi; *w.pren*, divisio prenasalis communis.

form type disappeared whereas certain others persisted and developed progressively, these phenomena might very well have led to such conditions as those found in Urodeles. There is thus nothing that actually contradicts the assumption that the dermal bones on the dorsal side of the snout in Urodeles are derived from certain definite bones in the ethmoidal shield of Porolepiform Crossopterygians.

Thus in most respects *Porolepiformes* and Urodeles display fundamental points of agreement as to the development of the snout. On several points the agreement is so important and detailed that it cannot possibly be explained as parallelism but must be due to very close genetic relations between the two groups. Though very little is known at present concerning the posterior parts of the skull in *Porolepiformes*, we are, I think, nevertheless justified in concluding that *Porolepiformes* and Urodeles are very closely related to each other and that the Urodeles must be derived either from primitive *Porolepiformes* or from ancestors very closely akin to them.

With our present knowledge of *Porolepiformes* and Urodeles we may imagine that the phyletic development of the Urodele snout from one of a Porolepiform type took place somewhat as follows (see fig. 46).

1) The endoskeleton to a large extent failed to ossify and thus became almost entirely secondarily cartilaginous. Bony tissue was retained in primitive Urodeles in the lateral nasal wall (the nariodal) and in the interorbital wall (the orbitosphenoid); in more advanced Urodeles in the interorbital wall only (the orbitosphenoid).

2) The endoskeleton became much reduced. The internasal ridge disappeared more or less completely (in certain Urodeles it is probably represented by a vestige, the cartilago infranasalis). The divisio prenasalis communis and an adjacent anterior part of the internasal wall became partly resorbed so as ultimately to be represented only by the paired thin prenasal wall, the paired processus prenasalis inferior lateralis, and the unpaired processus prenasalis superior medius. All the nasal walls decreased in thickness. The fenestrae endochoanalis and endonarina anterior widened in diameter. The dorsal and lateral walls of the nasal capsule were perforated by two new openings, the fenestra dorsalis nasi and the fenestra lateralis nasi, not present in *Porolepiformes*. The endocranial roof and floor of the part of the cranial cavity situated in the foremost part of the interorbital wall disappeared completely and so did the tectum orbitale. The pars autopalatina of the palatoquadrate was strongly reduced.

3) The dermal bones lost their superficial layers and due to this and to resorptions in the outer parts of the endoskeleton they gained a position fairly deep below the epidermis. Nerves and vessels primarily

passing below or in the dermal bones as well as the sensory canals thus became situated outside the dermal bones.

4) Despite the general tendency towards a reduction of the endoskeleton a progressive formation of cartilage took place in certain areas. A bar of cartilage arose between the fenestra endochoanalis and the large posterior part of the fenestra endonarina posterior. The latter fenestra was in certain forms also closed by cartilage. Finally in certain forms (*Ambystoma*), the crista rostro-caudalis was excessively developed in a ventro-medial direction so as to extend to and fuse with the solum nasi.

5) The posterior external nasal tube was lengthened backwards as far as to the eye and its posterior part moved somewhat upwards; the tube was thus transformed into the nasolachrymal duct. The fenestra endonarina posterior migrated in a direction forwards towards the fenestra endonarina anterior, and often fused with this into a fenestra endonarina communis. This migration caused a considerable shortening of the internal nasolachrymal groove (= the groove *gr. ntp* in *Porolepis*) so that a part of the nasolachrymal duct primarily lying almost entirely within the nasal cavity became at last to a large extent situated along the outer face of the lateral nasal wall. On this face it gave rise to the formation of an external nasolachrymal groove ("impressio conchalis") in which it passed backwards. The fenestra exonarina posterior migrated somewhat backwards and was at first transformed into a groove and ultimately into a closed canal. This canal, the canalis nasolacrimalis, primarily pierced the anterior parts of the lachrymal, but when this bone was reduced it perforated the "prefrontal" or became situated in the suture between the last-mentioned bone and the maxillary.

6) The nasal cavities widened in a medial direction, becoming lower and broader. This widening of the nasal cavities caused considerable modifications in the development of the medial parts of the ethmoidal region. The anterior parts of the medial nasal walls were pushed towards one another, which resulted in a narrowing of the cavum internasale. The lateral portion of the posterior part of the medial nasal wall — the part of the medial nasal wall separating the nasal cavity from the ethmoidal part of the cranial cavity — was reduced, and owing to this the canalis olfactorius was shortened and transformed into a fenestra olfactoria situated mainly in a transverse plane.

7) The brain was withdrawn from the ethmoidal region. The bulbi olfactorii retained their primary position in relation to the endocranium and in consequence of the withdrawal of the brain from the ethmoidal region they thus became situated further anteriorly in relation to the hemispheres than was primarily the case.

8) Some of the dermal bones of the snout were reduced whereas others persisted and underwent a progressive development. This progressive development has, however, taken place largely within the Urodele group itself and thus after the differentiation of this group from its Crossopterygian ancestors.

The pars facialis of the "premaxillary" and the similarly termed division of the maxillary increased in extent. The lateral rostral and at least the majority of the nasal and postrostral elements seem to have disappeared. The lachrymal also disappeared completely in more advanced Urodeles, but vestiges of this bone are still found in primitive Urodeles. The posterior tectal and one of the anterior tectals seem in Urodeles to persist as the "prefrontal" and "nasal" respectively. Another anterior tectal element was probably present in certain Urodeles as the "prenasal". The most posterior nasal or perhaps a posterior postrostral may have formed the "frontal" in Urodeles. The vomer increased in size through growth in two or three directions, viz. a) in a postero-lateral direction (the majority of Urodeles), b) in an antero-medial direction (*Triturus* and certain other forms), and c) possibly also in a caudal direction (e. g. *Salamandra*). This growth of the vomer caused the following changes respectively: a) The fenestra exochoanalis, primarily situated laterally to the antero-lateral part of the vomer, was displaced medially so as ultimately to form a notch in the posterior border of the vomer; b) the internasal and prenasal cavities became provided with a floor of dermal bone and the primary wide opening between the vomers of both sides, the anterior palatal fenestra, was reduced to a relatively small foramen or slit in the median suture formed by the vomers; c) a tooth-bearing posterior process from the vomer was possibly formed on the lower face of the parasphenoid. However, this process is perhaps not a real posterior outgrowth of the vomer, but a paired parasphenoid dental plate (like that of certain Crossopterygians and Urodeles) incorporated in the vomer. In certain Urodeles an ascending lamina was also developed on the vomer. Such a lamina had, however, arisen even in late representatives of the Porolepiform Crossopterygians (*Holoptychius*). The tooth-bearing median ridge of the parasphenoid was completely reduced. The dermopalatine disappeared in connection with the reduction of the anterior part of the palatoquadrate.

f. Comparison with Anura.

Whereas *Porolepiformes* and Urodeles show a great many points of fundamental and amazingly close agreement in the development of the snout, *Porolepiformes* and Anurans differ considerably from each other in this part of the skull. As we shall see below, the Anurans are in this respect fundamentally as the *Osteolepiformes.* The differences between them and the *Porolepiformes* are thus on the whole the same as those between *Porolepiformes* and *Osteolepiformes.* The reader is therefore referred to the exhaustive discussion below in the comparison between the two last-mentioned groups (pp. 488—495).

C. The snout in Osteolepiformes.

1. Descriptive section.

a. Eusthenopteron foordi Whiteaves.

(Figs. 34, 47—61, 64 A, 65 A, 67 A, 68 A, D, E, 70 A, 71 A, 72 A, 86 A, 87 A; pl. 6, figs. 1, 2; pls. 7—13).

Previous investigations. — The skull in *Eusthenopteron foordi* (as to other *Eusthenopteron* species see pp. 481—482 and fig. 62 A) has been dealt with by Whiteaves (1889), Hussakof (1912), Bryant (1919), Stensiö (1921, pp. 133—135, fig. 57; 1922 a, pp. 1249—1259, fig. 4), Woodward (1922), Watson (1926, pp. 195—199, 248—249, figs. 4 B, 34, 35), Aldinger (1931), Säve-Söderbergh (1932 a, fig. 19; 1933 a, pp. 108—109, pl. 15, fig. 1; pl. 16), Gregory and others (1935), Holmgren and Stensiö (1936, pp. 344—363, figs. 264 B, 269 A, 270 A, 273 A, B), Westoll (1937 c), and others. The structure of the snout has, however, remained very imperfectly known. In the restoration given by Bryant the ethmoidal region is not shown and this restoration is also incorrect in several respects. Holmgren and Stensiö (1936, fig. 264 B) published a restoration of the endocranium in lateral aspect, which is very diagrammatic as regards the foremost parts. The palatoquadrate was restored by Watson (1926, figs. 4 B, 34) and later on by Holmgren and Stensiö (1936, fig. 270 A), but the detailed development of its anterior parts is not shown in their restorations. Our knowledge of the dermal bones and the sensory canals of the snout has also been comparatively limited, and the previous restorations showing these structures are either incorrect in several respects or else incomplete (Bryant 1919, fig. 2; Stensiö 1922 a, fig. 4; Romer 1933, fig. 53 A; Gregory and others 1935, fig. 3 A; Holmgren and Stensiö 1936, fig. 273 A, B, etc.). The dermal skeleton of the palate was reconstructed by Bryant (1919, fig. 4) and Watson (1926, fig. 4 B; cf. figs. 34, 35; Romer 1933 fig. 53 B; Holmgren and Stensiö 1936, figs. 269 A, 270 A). The fenestra exochoanalis was correctly identified by Watson.

A brief account of the general disposition of the dermal bones and the sensory canals of the snout has been given above (pp. 334—353, fig. 34).

Material. — The subsequent description of the snout in *Eusthenopteron foordi* is based above all on drawings of two excellent series made with the aid of Sollas' grinding method. These two series, made possible by grants from the Swedish Government and from the Hierta-Retzius foundations, were made during the years of 1927—1938. They belong to the Swedish Museum of Natural History in Stockholm. Besides these drawings the writer has also used several specimens belonging to the Swedish Museum of Natural History, above all Nos. P. 341 and 383, and in addition two other specimens, one belonging to the Royal Scottish Museum in Edinburgh, No. 1897 51—201, and the other from Patten's collection (No. F. 5) in the possession of Dartmouth College, Hanover N. H., U. S. A. All the specimens are from the Escuminac formation of Magouasha, Scaumenac Bay in Canada, a formation which in all probability is of lower Upper Devonian age (cf. Jarvik 1937, pp. 120—122). One of the specimens used for grinding consisted of the anterior part of the divisio cranialis anterior including the ethmoidal region and the foremost part of the orbitotemporal region backwards about to the canal for the v. cerebralis anterior (*c. ca*, fig. 47 A, B). This specimen was well preserved anteriorly, but its hinder parts were badly crushed. My description of the foremost part of the ethmoidal region is chiefly based on the drawings of this specimen (gr.-ser. 1; pl. 11, figs. 1—5). The other specimen ground (gr.-ser. 2; pl. 11, fig. 6; pls. 12, 13) was a head of an almost complete individual which was extremely well preserved (spec. No. P. 222 in Swed. Mus. of Nat. Hist. in Stockholm). This head was complete except for the foremost part of the snout. The grinding of the two specimens was made practically at right angles to the longitudinal axis of the head. The sections were drawn with an interspace of 0.2 mm and a magnification of × 10.

The two specimens ground differ somewhat from one another, for instance by the septum nasi being somewhat thinner in No. P. 222 used for gr.-ser. 2 than in the one used for gr.-ser. 1, and it is not impossible, therefore, that these specimens may belong to two different species (cf. Säve-Söderbergh 1933 a, p. 108). Differences are also found in the development of the dermal skeleton in various specimens, but considering the large material examined these differences do not justify the distinguishing of a new species. In these circumstances all the *Eusthenopteron* material from Scaumenac Bay is here referred to *E. foordi* Whiteaves.

The restorations of the snout in *E. foordi* given in the present work are based as far as possible on the specimen used for gr.-ser. 2 (No. P. 222). The data concerning magnification refer, therefore, to specimen No. P. 222 which is in all respects the most complete and best preserved specimen of the species so far known. It is medium-sized, its total length from tip of snout (including the missing part) to tip of caudal fin must have been approx. 530 mm, of which the ethmoidal region as here defined (p. 245) covers about 18 mm only.

Description. — The subsequent account will deal principally with the ethmoidal region of the endocranium. Both the ethmoidal region and the endocranium otherwise were cartilaginous in young individuals and became ossified comparatively late. In medium-sized and fully mature individuals the ethmoidal region is normally well ossified, but as shown by the large material at my disposal, it sometimes remained cartilaginous or slightly ossified also in such individuals. As in *Porolepis* the ossification in the ethmoidal region is continuous with that in the orbitotemporal region and forms with this the large ethmosphenoid bone (*Etsph*, fig. 34; pl. 10).

In an ossified condition the ethmoidal region, like the other parts of the endoskeleton, is made up of cancellated bony tissue which on its exposed faces and in all canals and cavities is lined with a periostal bone layer. This periostal bone layer is very thin, however, on all the areas overlapped by dermal bones. In the grinding series it is seen that there is usually a low interspace between the endocranium and the dermal bones outside it (figs. 53, 58; pls. 11—13), which probably was occupied by connective tissue. In certain cases, however, the dermal bones rest directly on the endocranium. The latter condition is certainly secondary in most cases and due to compression of the specimens, but it is highly probable that connective tissue was actually absent in places and that at these places a slight growing together occurred between the dermal bones and the endocranium.

In the two specimens examined by the grinding method and also in several other specimens there are certain superficial areas which were slightly ossified or cartilaginous. An area of this sort (*cart*) is met with on the postero-lateral part of the ethmoidal region in specimens Nos. P. 341 (pl. 7, fig. 2; pl. 8, fig. 2) and P. 222 (gr.-ser. 2; pl. 12, figs. 4—6; pl. 13, fig. 1). In the latter specimen we find a wide interspace between the dermal bones and the endocranium which is devoid of an external periostal bone layer at this place. In specimen No. P. 341 the corresponding interspace is somewhat smaller and occupied by crystals of calcite. The approximate extent of the unossified area in question is shown in several of the restorations (*cart*, figs. 47 A, B, 49, 50, 70 A). The anterior part of the lateral nasal wall (lamina nariochoanalis) was also imperfectly ossified in the two specimens just referred to.

The ethmoidal region covers somewhat more than one third of the length of the ethmosphenoid bone and a little more than one fifth of the total length of the endocranium. The region is broader than long, but longer than high, the proportions between its breadth, length and height being approx. 11 : 9 : 7. It is both broadest and highest in its posterior part. The breadth decreases only slightly forwards, the rostral end being comparatively broad. The height is largest at and near the transition of the region into the interorbital wall from where it decreases considerably both forwards and towards the sides.

The faces of the ethmoidal region are three in number, an unpaired dorsal one, an unpaired ventral one, and a paired posterior one. The dorsal face (fig. 47), which is covered by the ethmoidal shield, is strongly arched both in rostro-caudal and transverse directions and forms not only the dorsal boundary of the region, but also its anterior and lateral boundaries. The ventral face (fig. 48), is directed somewhat forwards and is to a large extent covered by the dermal bones of the palate. The posterior face of the ethmoidal region (figs. 49, 50) forms the posterior face of the postnasal wall of either side. The nasal cavity is comparatively small and situated in the postero-lateral part of the region. The internasal wall (*w. in*, figs. 57 A, 70 A) is solid and forms a nasal septum (*sn*, figs. 51—53, 57 B, 59, 71 A). The divisio prenasalis communis (*w. pren*, figs. 57 A, 67 A, 70 A, 72 A), which constitutes the rostral part of the ethmosphenoid bone, is somewhat longer than in *Porolepis*. This division is produced postero-laterally on either side into an obtuse short process, the crista subnasalis (*cr. sbn*, figs. 47 B, C, 48), directed ventrally, whereas anteriorly it forms an unpaired broad rostral process, the dorsal rostral process (*pr. rd*, figs. 47, 48). The postnasal wall (*w. pn*, figs. 48, 50, 51, 59) occupies an almost transverse position between the nasal cavity and the orbit. The longer lateral part of its ventral margin is free and is produced laterally in a ventral direction so as to constitute a short process directed downwards, the postero-ventral process (*pr. pv*, figs. 47 B, 48—50), which forms the very postero-ventro-lateral corner of the ethmoidal region. The nasal cavity is surrounded by well developed walls, the nasal capsule being fairly complete. The lateral nasal wall is pierced by the fenestra endonarina anterior (*fe. ena*, fig. 47) whereas the floor is to a large extent occupied by the large fenestra endochoanalis (*fe. ench*, figs. 47 C, 48). The dorso-medial margin of the lamina nariochoanalis (*la. nch*, figs. 47, 48) projects medially into the nasal cavity as a strong process, the processus intermedius (*pr. im*, figs. 47 B, 52, 53). The fenestra endonarina posterior (*fe. enp*, figs. 49—51) lies in the ventro-lateral part of the postnasal wall.

The anterior part of the orbitotemporal region nearest behind the ethmoidal region consists of a high, comparatively narrow interorbital wall and an imperfectly developed tectum orbitale. The interorbital wall is thickened somewhat above its middle where it lodges the foremost part of the cranial cavity (*p. bulb*, figs. 49, 57 A—C) and the paired canalis olfactorius (*c. olf*, figs. 50, 57 A—C, 59), while both dorsally and ventrally to this part it is thin and solid ($s_{d}io$, $s_{v}io$, figs. 47 A, B, 48, 49, 50). The ventro-lateral edge of the foremost portion of the thin ventral part forms a low lateral ledge on either side, the anterior suborbital ledge (*sh. sbo*, figs. 47 B, 48, 49, 50), which anteriorly meets the lateral edge of the solum nasi at a distinct angle, forming the postero-ventro-medial corner of the ethmoidal region (*co. pm*, figs. 47 C, 48—50). The tectum orbitale is represented by a thin lamina, the lamina supraorbitalis (*la. so*, figs. 47—50), which projects backwards from the uppermost part of the postnasal wall, and by a narrow ledge, which protrudes laterally along the dorso-lateral margin of the interorbital wall and increases somewhat in breadth forwards (figs. 47, 50) passing over anteriorly into the supraorbital lamina. The supraorbital lamina is continued backwards by a long narrow process, the lateral supraorbital process (*pr. sol*, figs. 47—50).

The ethmoidal shield covering the dorsal face of the ethmoidal region is pierced by the fenestra exonarina anterior (*fe. exa*, figs. 34, 52 B, 68 A). No fenestra exonarina posterior is developed. The ethmoidal shield consists of numerous dermal bones (cf. pp. 346—352, and figs. 34, 68 A), but only the lateral rostral and anterior tectal will be treated here (concerning the naso-rostro-premaxillary see pp. 496—498; fig. 68 D, E). As in *Porolepis*, the ethmoidal shield is provided with a palatal lamina (*la. pal*) which covers a marginal zone of the ventral face of the ethmoidal region. The rest of the ventral face of the region is covered by the parasphenoid and the vomers (see pp. 450—451, 498—500) except an unpaired short and broad anterior area exposed in a gap between the dermal bones, the anterior palatal fenestra (*fe. pal*, figs. 56, 64 A, 87 A). The anterior palatal fenestra lies in a large pit or depression, the fossa apicalis (*fo. ap*), which is well bounded off from the other more posterior parts of the roof of the mouth cavity. The fenestra exochoanalis (*fe. exch*, figs. 56, 87 A) lies below the fenestra endochoanalis, laterally to the vomer of its side.

As pointed out by Holmgren and Stensiö (1936, p. 353) the palatoquadrate is a single ossification. Watson's statement (1925, p. 860; 1926, pp. 248—249) that it consists of several ossifications is erroneous. In this work I shall discuss only the pars autopalatina (*Aup*, figs. 54, 55, 64 A, 65 A, 70 A) of the palatoquadrate ossification.

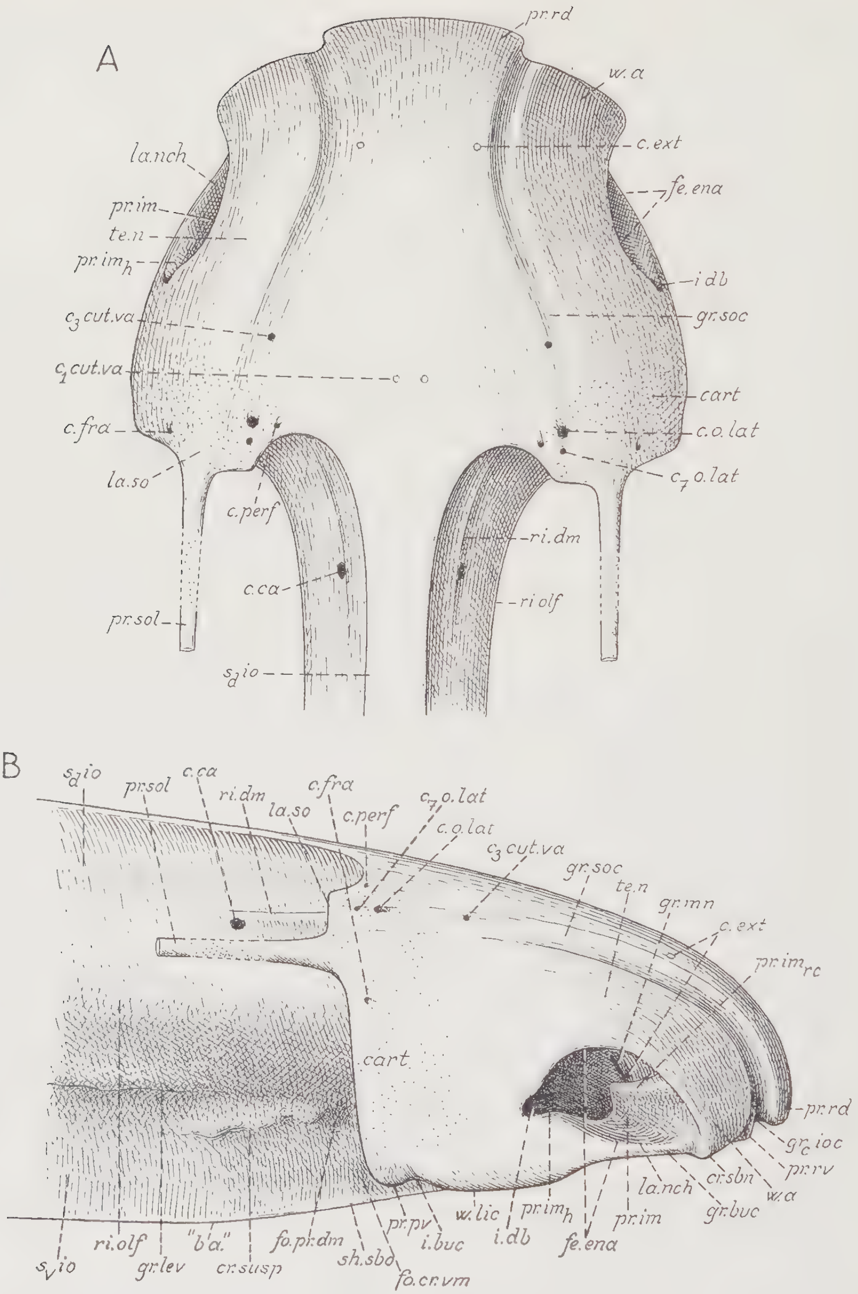
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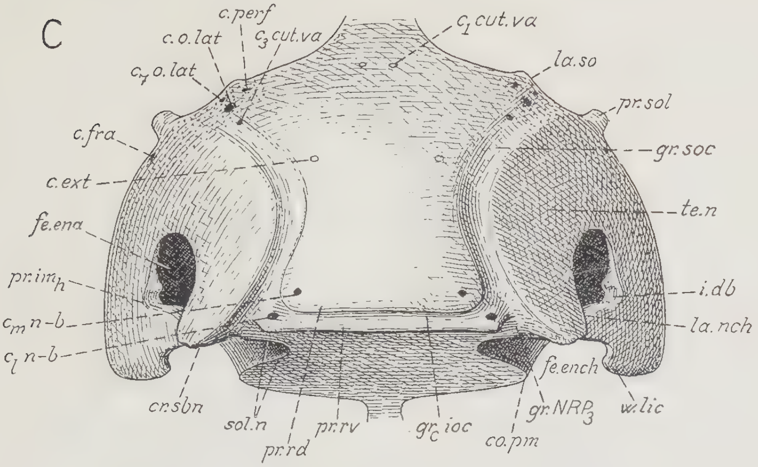
Fig. 47. *Eusthenopteron foordi* Whiteaves. The anterior parts of the ethmosphenoid, comprising the ethmoidal region and an adjacent anterior part of the orbitotemporal region of the endocranium. *A*, dorsal, *B*, lateral, *C*, anterior aspect. Cartilage dotted. Restorations mainly after grinding-series 1 and 2. $^{10}/_{3}$.

"*ba*", "basal angle"; *cart*, superficial part of endocranium probably formed of cartilage; *c. ca*, canal for v. cerebralis anterior; *c. ext*, canal for r. externus narium of n. profundus;



c. fra, canal for r. frontalis anterior of n. profundus; $c_l n$ *b*, $c_m n$-*b*, lateral and medial branches of nasobasal canal; *c. o. lat,* canal for r. ophthalmicus lateralis; *co. pm,* postero-ventro-medial corner of ethmoidal region; *c. perf,* canal for r. frontalis perforans of n. profundus; *cr. sbn.* crista subnasalis; *cr. susp,* crista suspendens; c_1*cut. va*, c_3*cut. va*, first and third branches of canal for cutaneous vessel; c_7*o. lat,* canal for branch of r. ophthalmicus lateralis to canal organ in nasal 7; *fe. ena,* fenestra endonarina anterior; *fe. ench,* fenestra endochoanalis; *fo. cr. vm,* pit receiving ventro-medial crista of pars autopalatina; *fo. pr. dm,* pit for dorso-medial process of pars autopalatina; *gr. buc,* groove for r. buccalis lateralis; gr_c*ioc,* groove for ridge on dorsal face of pars palatina of naso-rostro-premaxillary, lodging ethmoidal commissure of infraorbital sensory canals; *gr. lev,* groove for origin of principal portion of m. levator bulbi; *gr. mn,* groove for r. medialis narium of n. profundus; *gr.* NRP_3, groove for the ridge *ri.* NRP_3 on dorsal face of pars palatina of naso-rostro-premaxillary; *gr. soc,* groove for supraorbital sensory canal ridge; *i. buc,* notch for r. buccalis lateralis; *i. db,* notch for the processes of the lateral rostral and anterior tectal that extend into nasal cavity; *la. nch,* lamina nariochoanalis; *la. so,* lamina supraorbitalis; *pr. im,* processus intermedius of lamina nariochoanalis; *pr.* im_h, *pr.* im_{rc}, posterior horizontal and anterior recurved portions of processus intermedius; *pr. pv,* postero-ventral process of ethmoidal region; *pr. rd, pr. rv,* dorsal and ventral rostral processes; *pr. sol,* processus supraorbitalis lateralis; *ri. dm,* dorso-medial ridge on posterior face of postnasal wall and on adjacent part of lateral face of interorbital wall; *ri. olf,* olfactory ridge; s_d*io,* thin dorsal part of interorbital wall; *sh. sbo,* anterior suborbital ledge; *sol. n,* solum nasi; s_v*io,* thin ventral part of interorbital wall; *te. n,* tectum nasi; *w. a,* prenasal wall; *w. lic,* ventral medially curved part of lateral nasal wall.

After this brief general orientation I shall now enter in detail upon the development of the snout, turning first to the external faces of the ethmoidal region.

The dorsal face of the ethmoidal region (figs. 47, 51—53, 58, 59, 67 A, 68 A, 71 A; pl. 7, fig. 2; pls. 11, 12; pl. 13, figs. 1—3) has very much the same shape as the ethmoidal shield covering it. It is fairly plane and about horizontal in its posterior median part, which forms a direct anterior continuation of the dorsal face of the interorbital wall. Anteriorly and laterally it curves strongly downwards so as to be directed almost straight forwards and laterally respectively. As pointed out above (p. 427), there is at least in certain specimens an area (*cart*) on the postero-lateral part of the dorsal face of the ethmoidal region that was imperfectly ossified or completely cartilaginous. The face presents a paired, somewhat S-shaped groove, *gr. soc* (figs. 47, 48, 51, 52 A, 58; pl. 7, fig. 2; pl. 11, fig. 3; pl. 12, fig. 2), for the paired supraorbital sensory canal ridge (*ri. soc*, figs. 52 B, 58) on the lower face of the fronto-ethmoidal shield. This groove begins posteriorly on the lamina supraorbitalis close medially to the base of the processus supraorbitalis lateralis (*pr. sol*) and as shown in fig. 47 it runs forwards to the very rostral end of the endocranium. It is shallow posteriorly but increases in depth forwards and at its anterior end causes a distinct notch in the rostral margin of the ethmoidal region. The part of the divisio prenasalis communis situated between the pair of notches constitutes the short and broad dorsal rostral process (*pr. rd*, figs 47, 48; cf. *gr. pr. rd*, fig. 68 E) referred to above. Besides the fenestra endonarina anterior (*fe. ena*; see p. 446) the dorsal face presents several foramina (*c. o. lat*, *c. perf*, *c. ext*, etc.) which are the anterior or dorsal orifices of canals passing forwards onto the ethmoidal region or ascending through that region (see pp. 469—471; in the cases when these canals could not be traced to or almost to the very dorsal face of the ethmoidal region the approximate position of their dorsal orifices is indicated by small circles, for instance *c. ext* in fig. 47).

The ventral face of the ethmoidal region (figs. 47 C, 48, 51—53, 56, 58; pl. 8, fig. 1; pl. 9, fig. 3; pls. 11, 12) is directed downwards and a little forwards. It passes over posteriorly into the ventral face of the interorbital wall.[1] Its postero-lateral part is occupied by the large fenestra endochoanalis (*fe. ench*; pp. 447—448) which stretches laterally and backwards to the ventral edges of the lateral and posterior nasal walls. To facilitate the description the face may be regarded as composed of two divisions, one anterior and one posterior.

The anterior division forms the ventral face of the divisio prenasalis communis and of the anterior parts of the solum nasi of either side. Most rostrally on this division is a distinct transverse groove, *$gr_c ioc$* (figs. 47 B, C, 48), caused by the ridge (*$ri_c ioc$*. fig. 68 D; pl. 11, fig. 1) on the dorsal side of the pars palatina (*NRP_3*) of the naso-rostro-premaxillary that houses the ethmoidal commissure (*socc*, fig. 68 D) of the infraorbital sensory canals. This groove is continuous laterally with the rostral end of the groove *gr. soc* on the dorsal face of the ethmoidal region and forms the morphological ventral boundary of the dorsal rostral

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[1] The ventral face of the interorbital wall is directed slightly forwards in its anterior part, but straight downwards in its posterior part. Between its anterior and posterior parts we thus find, as in *Porolepis* (cf. p. 358), an obtuse angle ("*ba*", fig. 47 B, C) which reminds of the basal angle in Selachians, but which lies relatively further anteriorly on the orbitotemporal region than that angle.

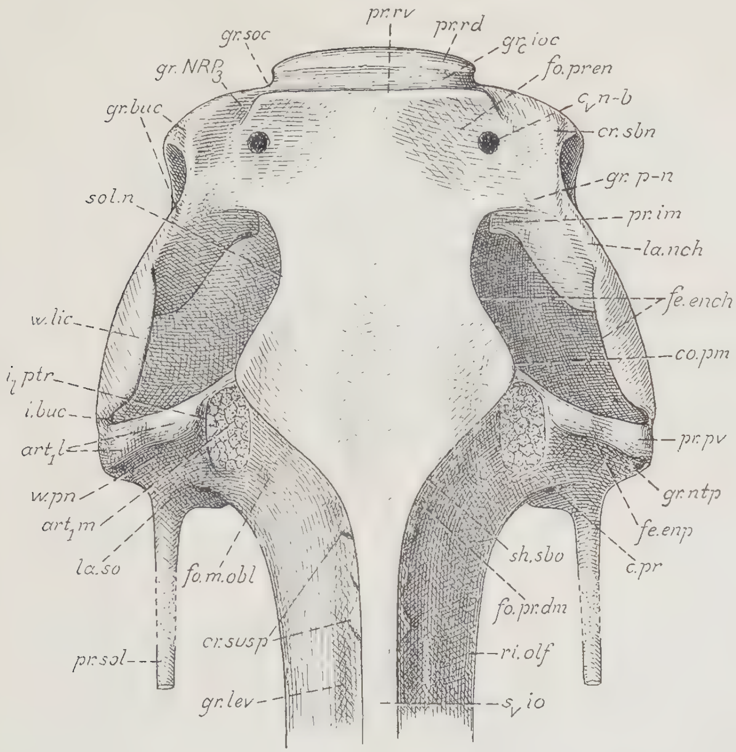


Fig. 48. *Eusthenopteron foordi* Whiteaves. Same part of the endocranium as in fig. 47. Ventral view. $^{10}/_3$.

art_1l, art_1m, lateral and medial autopalatine articular areas; *co. pm,* postero-ventro-medial corner of ethmoidal region; *c. pr,* profundus canal; *cr. sbn,* crista subnasalis; *cr. susp,* crista suspendens; c_vn-b, ventral branch of nasobasal canal; *fe. ench,* fenestra endochoanalis; *fe. enp,* opening in postnasal wall, probably representing fenestra endonarina posterior; *fo. m. obl,* pit for origin of oblique eye muscles; *fo. pr. dm,* pit receiving dorsomedial process of pars autopalatina; *fo. pren,* prenasal pit; *gr. buc,* groove for r. buccalis lateralis; gr_cioc, groove for ridge on dorsal face of pars palatina of naso-rostro-premaxillary lodging ethmoidal commissure of infraorbital sensory canals; *gr. lev,* groove for origin of principal portion of m. levator bulbi; $gr. NRP_3$, groove for ridge $ri. NRP_3$ on dorsal face of pars palatina of naso-rostro-premaxillary; *gr. ntp,* groove, probably for posterior nasal tube; *gr. p-n,* groove for r. palatonasalis; *gr. soc,* groove for supraorbital sensory canal ridge; *i. buc,* notch for r. buccalis lateralis; $i_lp. tr$, notch forming lateral wall of pit for insertion of portio transversalis of m. levator bulbi; *la. nch,* lamina nariochoanalis; *la. so,* lamina supraorbitalis; *pr. im,* processus intermedius of lamina nariochoanalis; *pr. pv,* postero-ventral process of ethmoidal region; *pr. rd, pr. rv,* dorsal and ventral rostral processes; *pr. sol,* processus supraorbitalis lateralis; *ri. olf,* olfactory ridge; *sh. sbo,* anterior suborbital ledge; *sol. n,* solum nasi; s_vio, thin ventral part of interorbital wall; *w. lic,* ventral medially curved part of lateral nasal wall; *w. pn,* postnasal wall.

process (*pr. rd*). The postero-ventral boundary of the groove itself consists of a short and broad lamina, the ventral rostral process (*pr. rv*, figs. 47 B, C, 48; cf. *gr. pr. rv*, fig. 68 D). At either lateral end of the transverse groove gr_cioc issues a short groove, $gr. NRP_3$, in a postero-lateral direction. This groove, which becomes shallower backwards, was occupied by a dorsal ridge, $ri. NRP_3$ (figs. 68 D, 72 A; pl. 9, fig. 3; pl. 11, figs. 1, 2), on the postero-lateral part of the pars palatina of the naso-rostro-premaxillary. Laterally to the groove $gr. NRP_3$ there is a rostro-caudal ridge projecting ventrally and formed by the most latero-ventral part of the divisio prenasalis communis. This ridge, which is the crista subnasalis (*cr. sbn*, figs. 47 B, C, 48, 52 A, 71 A; pl. 9, fig. 3; pl. 11, fig. 1) referred to above, decreases in height forwards. Posteriorly it ends with a small vertical face directed backwards. It lies in a groove on the dorsal side of the pars palatina of the naso-rostro-premaxillary, a groove bounded antero-laterally by the pars facialis (NRP_2) of the naso-rostro-premaxillary and postero-medially by the ridge $ri. NRP_3$ (cf. fig. 68 D). The lateral side of the crista subnasalis is provided with a rostro-caudal groove (*gr. buc*, figs. 47 B, 48, 52 C) which is the anterior part of a groove for the r. buccalis lateralis (cf. p. 472). In certain specimens this groove is represented by a rostro-caudal canal (*c. buc*, pl. 9, fig. 4). Medially to the crista subnasalis and posteriorly to the ventral rostral process lies a wide, shallow depression, which forms part of the prenasal pit to be described below (p. 459; *fo. pren*, figs. 48, 56, 64 A; pl. 8, fig. 1; pl. 11, fig. 2). This depression is separated from the corresponding one of the opposite side by a broad median rostro-caudal ridge. Its anterior part is exposed in the unpaired short broad gap in the dermal skeleton of the palate referred to above as the anterior palatal fenestra (*fe. pal*, figs. 56, 64 A, 87 A; pl. 8, fig. 1; pl. 11, fig. 2), whereas its posterior part is covered by the thin antero-lateral corner of the vomer. At the bottom of the prenasal pit lies a fairly large foramen which is the orifice of the ventral branch ($c_v n\text{-}b$) of the nasobasal canal to be described below (p. 470). Somewhat postero-laterally to this foramen is the anterior end of a shallow indistinct groove (*gr. p-n*, figs. 48, 52 A) which leads forwards and somewhat medially from the antero-lateral part of the fenestra endochoanalis and forms the roof of a canal, the anterior palatonasal canal ($c_a pal$, see p. 473), covered by dermal bones ventrally.

The posterior division of the ventral face of the ethmoidal region (fig. 48) includes both the ventral face of the internasal wall and the ventral face of the posterior medial parts of the solum nasi of either side. The anterior part of the division is plane, but its posterior part presents two shallow depressions, a long median unpaired one, and a fairly short lateral paired one at the postero-ventro-medial corner (*co. pm*) of the ethmoidal region. These two depressions are occupied by dorsal thickenings of the parasphenoid and vomers respectively (pl. 12, figs. 1—4).

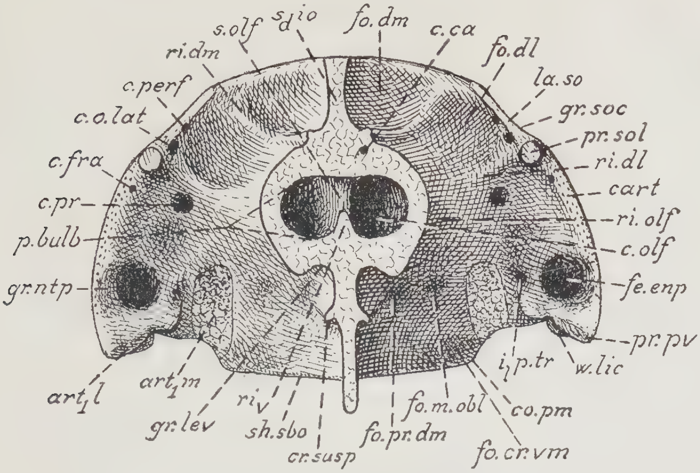


Fig. 49. *Eusthenopteron foordi* Whiteaves. The anterior part of the endocranium in posterior aspect, showing the posterior faces of the postnasal walls. The endocranium cut off behind the transverse plane through the orbital opening of the canal for the v. cerebralis anterior. Restoration mainly after grinding-series 2. Cartilage dotted. $^3/_1$.

art_1l, art_1m, lateral and medial autopalatine articular areas; *cart*, area of endrocranium, probably slightly ossified or cartilaginous; *c. ca*, canal for v. cerebralis anterior; *c. fra*, canal for r. frontalis anterior of n. profundus; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *co. pm*, postero-ventro-medial corner of ethmoidal region; *c. perf*, canal for r. frontalis perforans of n. profundus; *c. pr*, profundus canal; *cr. susp*, crista suspendens; *fe. enp*, opening, probably representing fenestra endonarina posterior; *fo. cr. vm*, pit receiving ventro-medial crista of pars autopalatina; *fo. dl*, *fo. dm*, dorso-lateral and dorso-medial depressions in posterior face of postnasal wall; *fo. m. obl*, pit for origin of oblique eye muscles; *fo. pr. dm*, pit receiving dorso-medial process of pars autopalatina; *gr. lev*, groove for origin of principal portion of m. levator bulbi; *gr. ntp*, groove for posterior external nasal tube; *gr. soc*, groove for supraorbital sensory canal ridge; $i_1p.tr$, notch forming lateral wall of pit for insertion of portio transversalis of m. levator bulbi; *la. so*, lamina supraorbitalis; *p. bulb*, bulbar portion of cranial cavity; *pr. pv*, postero-ventral process of ethmoidal region; *pr. sol*, processus supraorbitalis lateralis; *ri. dl*, *ri. dm*, dorso-lateral and dorso-medial ridges on posterior face of postnasal wall; *ri. olf*, olfactory ridge; ri_v, median ridge ascending from floor of cranial cavity; s_dio, thin dorsal part of interorbital wall; *sh. sbo*, anterior suborbital ledge; *s. olf*, median septum separating olfactory canals; *w. lic*, ventral medially curved part of lateral nasal wall.

The paired posterior face of the ethmoidal region (figs. 49, 50, 55, 65 A; pl. 8, fig. 2; pl. 9, fig. 3; fig. 10, fig. 1) forms the posterior face of the postnasal wall of either side (*w. pn*) and passes over medially into the lateral face of the interorbital wall. It is directed practically straight backwards in its lateral part, somewhat postero-laterally and postero-dorso-laterally in its dorso-medial part, and postero-ventrally in its ventro-medial part. In the middle of the medial part of the face is the foremost end of a strong horizontal ridge, the olfactory ridge (*ri. olf*, figs. 47 A, B, 48—50, 65 A; pl. 8, fig. 2; pl. 10, fig. 1; pl. 13, figs. 4, 5), which continues backwards on the lateral face of the interorbital wall almost to the opticus canal (*c. II*, pl. 10). On the outside of the foremost part of the ridge there is a longitudinal depression (see fig. 65 A; pl. 13, figs. 3, 4), probably the place of origin for a portion (portio transversalis; see p. 524) of the m. levator bulbi. This depression is, however, distinctly developed in certain specimens only.

Dorsally to the olfactory ridge the posterior face of the ethmoidal region presents two depressions, a shallow dorso-medial one (*fo. dm*), and a somewhat deeper dorso-lateral one (*fo. dl*, figs. 49, 50; pl. 8, fig. 2; pl. 10; pl. 13, figs. 2, 3). The two depressions, fairly rounded in outline, are separated by a low, narrow ridge, the dorso-medial ridge (*ri. dm*, figs. 47 A, B, 49, 50; pl. 8, fig. 2; pl. 10; pl. 13, figs. 3—5), which continues backwards onto the interorbital wall, where it passes close above the olfactory ridge and terminates somewhat behind the external orifice of the canal (*c. ca*) for the v. cerebralis anterior. The dorsal and dorso-lateral boundaries of the depressions are formed by the lamina supraorbitalis (*la. so*, figs. 47 A, B, 48—50; pl. 8, fig. 2; pl. 10; pl. 13, fig. 3), which was well developed in specimen P. 222 used for gr.-ser. 2. In other specimens it is not so well represented. The posterior continuation of this lamina, the processus supraorbitalis lateralis (*pr. sol*, figs. 47 A—C, 48—50; pl. 13, figs. 4, 5), is almost circular in transverse sections. In gr.-ser. 2 it is interrupted in its middle part, where it probably was unossified. No processus supraorbitalis medialis (cf. p. 481) was present in specimen P. 222, but it is not impossible that such a process was developed in other individuals.

In the dorso-lateral part of the dorso-lateral depression (*fo. dl*), immediately below the basal part of the lamina supraorbitalis we find a foramen which is the posterior orifice of the canal for the r. ophthalmicus lateralis (*c. o. lat*, figs. 49, 50; pl. 7, fig. 2; pl. 8, fig. 2; see p. 471). Dorso-medially to this we notice another smaller foramen, which is the posterior opening of a canal (*c. perf*, figs. 49, 50; pl. 8, fig. 2) presumably for the r. frontalis perforans of the n. profundus (p. 471). Close ventro-laterally to the dorso-lateral depression (*fo. dl*) and separated from this by a ridge, the dorso-lateral ridge (*ri. dl*, figs. 49, 50, 65 A; pl. 8, fig. 2; pl. 10; pl. 13, fig. 3), lies the posterior orifice of the profundus canal (*c. pr*, figs. 48—50; pl. 8, figs. 1, 2; pl. 10; see p. 470). Laterally and slightly dorsally to this, at the very dorsal margin of the postnasal wall, is the posterior orifice of a narrow canal (*c. fra*, figs. 49, 50; pl. 8, fig. 2), conceivably for the r. frontalis anterior of the n. profundus (cf. p. 471). The postero-ventro-lateral part of the postnasal wall is pierced by a wide foramen (*fe. enp*) which presumably represents a fenestra endonarina posterior (see p. 446). This foramen opens posteriorly into a funnel-like depression on the posterior face of the ethmoidal region. Its ventro-medial boundary is a comparatively thin skeletal bridge which is produced ventrally into two short obtuse ventral processes, one lateral and one medial, separated by a shallow depression. The lateral process is the postero-ventral process (*pr. pv*, figs. 47 B, 48—50; pl. 13, fig. 2) of the ethmoidal region referred to above. The lower side of the skeletal bridge here in question has a special facet, the lateral autopalatine articular area (art_1l, figs. 48—50, 65 A; pl. 13, figs. 2, 3), against which abuts a correspondingly shaped facet (art_2l, fig. 54; cf. pp. 453, 456) of the pars autopalatina of the palatoquadrate. The facet art_1l is directed postero-ventro-medially. It extends from the medial side of the postero-ventral process, where it is most distinctly developed, across the depression in the middle part of the skeletal bridge onto the medial ventral process. The funnel-like depression around the presumed fenestra endonarina posterior is bounded medially by a distinct dorso-ventral ridge which in posterior aspect shows a semicircular notch (*ip. tr*, figs. 49—50; pl. 13, fig. 2; cf. p. 456) in the upper part of its medial margin. Medially to the ridge and thus on the postero-ventrally directed part of the posterior face of the ethmoidal region and close to the antero-ventral part of the interorbital wall there is a somewhat depressed articular area, the medial autopalatine articular area (art_1m, figs. 48—50, 65 A; pl. 8, figs. 1, 2; pl. 9, fig. 3; pl. 13, figs. 1—3). This area is very distinct, and unlike the lateral autopalatine articular area it is devoid of a lining of periostal bone. It is higher than broad and extends from immediately beneath the foremost part of the olfactory ridge forwards and downwards to the postero-medial margin of the fenestra endochoanalis. Its dorsal (postero-dorsal) end, which is somewhat more strongly depressed than the ventral (antero-ventral) end, was in contact with the upper end of the processus apicalis (*pr. ap*, figs. 54, 55) of the pars autopalatina (cf. p. 456).

Postero-ventrally to the medial autopalatine articular area at the transition between the postnasal and interorbital walls are found two wide and fairly shallow pits, one ventral and one dorsal. The ventral pit, *fo. cr. vm* (figs. 47 B, 49, 50; pl. 8, fig. 2; pl. 12, fig. 6; pl. 13, figs. 1, 2), is not confined to the endocranium only, but also extends forwards and downwards across the anterior suborbital ledge (*sh. sbo*, figs. 47 B, 48—50) onto the dorsal face of the vomerine shelf (*sh. Vo*, figs. 50, 56; pl. 8, figs. 1, 2; pl. 12, figs. 5, 6), a part of the vomer that protrudes postero-laterally to the ventral face of the endocranium. It receives the ventro-medial crest of the pars autopalatina (*cr. vm*, fig. 64 A). The dorsal pit, *fo. m. obl* (figs. 48—50, 55, 65 A; pl. 8, fig. 2), is probably the place of origin of the oblique muscles of the eye. Somewhat posteriorly to the dorsal pit, on the foremost part of the lateral face of the interorbital wall, lies a

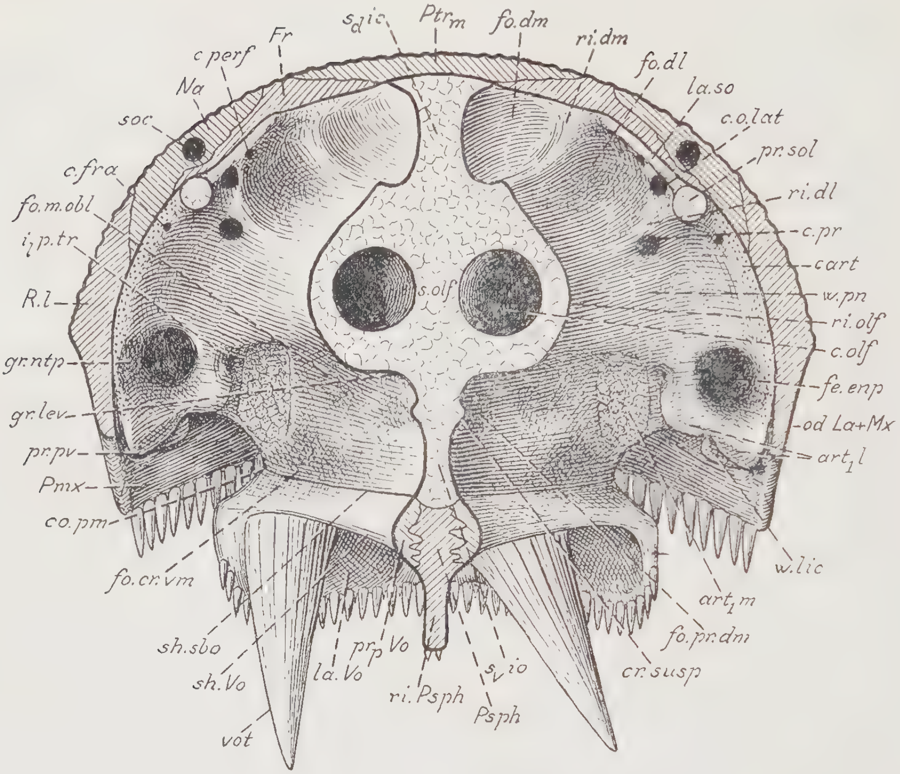


Fig. 50. *Eusthenopteron foordi* Whiteaves. Anterior part of divisio cranialis anterior in posterior aspect. Interorbital wall cut off slightly behind the postnasal wall, in front of the canal for the vena cerebralis anterior. The dermal bones shown in their position in relation to the endocranium. Restoration based on several specimens and on grinding-series 2. Cartilage dotted. Cross-sections through cartilage-bone and areas devoid of periostal bone reticulate. 4/1.

Fr, frontal; *Na*, nasal; *Pmx*, premaxillary; *Psph*, parasphenoid; Ptr_m, posterior median postrostral; *R. l*, supraorbito-tectal; $art_1 l$, $art_1 m$, lateral and medial autopalatine articular areas; *cart*, area of endocranium, probably slightly ossified or cartilaginous; *c. fra*, canal for r. frontalis anterior of n. profundus; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *co. pm*, postero-ventro-medial corner of ethmoidal region; *c. perf*, canal for r. frontalis perforans of n. profundus; *c. pr*, profundus canal; *cr. susp*, crista suspendens; *fe. enp*, opening, probably representing fenestra endonarina posterior; *fo. cr. vm*, pit receiving ventro-medial crista of pars autopalatina; *fo. dl*, *fo. dm*, dorso-lateral and dorso-medial depressions in posterior face of postnasal wall; *fo. m. obl*, pit for origin of oblique eye muscles; *fo. pr. dm*, pit receiving dorso-medial process of pars autopalatina; *gr. lev*, groove for origin of principal portion of m. levator bulbi; *gr. ntp*, groove for posterior nasal tube; $i_l p. tr$, notch forming lateral wall of pit for insertion of portio transversalis of m. levator bulbi; *la. so*, lamina supraorbitalis; *la. Vo*, vertical tooth-bearing lamina of vomer; *od. La + Mx*, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *pr. pv*, postero-ventral process of ethmoidal region; $pr_p Vo$, posterior process of vomer; *pr. sol*, processus supraorbitalis lateralis; *ri. dl*, *ri. dm*, dorso-lateral and dorso-medial ridges on posterior face of postnasal wall; *ri. olf*, olfactory ridge; *ri. Psph*, ventral tooth-bearing ridge of parasphenoid; $s_d io$, thin dorsal part of interorbital wall; *sh. sbo*, anterior suborbital ledge; *sh. Vo*, vomerine shelf; *soc*, supraorbital sensory canal; *s. olf*, median septum separating olfactory canals; $s_v io$, thin ventral part of interorbital wall; *w. lic*, ventral medially curved part of lateral nasal wall; *vot*, vomerine tusk; *w. pn*, postnasal wall.

third pit, *fo. pr. dm* (figs. 47 B, 48—50), which is somewhat smaller than the other two. This pit, which sometimes may be obscure, is developed for the dorso-medial process of the pars autopalatina of the palatoquadrate (*pr. dm*, fig. 54). Immediately behind it the thin ventral part (s_vio) of the interorbital wall has a well developed lateral crest running backwards and slightly downwards, the crista suspendens (*cr. susp*, figs. 47 B, 48—50, 55, 67 A; pl. 8, figs. 1, 2; pl. 10; pl. 13, fig. 5). The ventral side of this crest is grooved in a longitudinal direction and was in contact with the dorso-medial margin of the pars autopalatina of the palatoquadrate (see pp. 454—456). In certain individuals, as in the one used for gr.-ser. 2, it is a continuous formation throughout its length, whereas in others it is subdivided into a row of processes (pl. 10). Above the crista suspendens in the angle between the olfactory ridge and the thin ventral part of the interorbital wall is a well-marked rostro-caudal groove (*gr. lev*, figs. 47 B, 48—50; pl. 10; pl. 13, figs. 4—5) which opens lateroventrally and is bounded laterally by a ventral ridge-like formation or a longitudinal row of small processes along the lower part of the olfactory ridge. It was probably the place of origin of the principal portion of the m. levator bulbi (see p. 525).

After this description of the principal external faces of the endocranium of the snout we shall next turn to the walls of the nasal cavity.

The septum nasi (*sn*, figs. 51, 52 A, C, 53, 57 B, 59, 71 A; pl. 11, fig. 5; pl. 12, fig. 4; cf. *w. in*, fig. 70 A) is comparatively thick. It was thicker in the specimen used for gr.-ser. 1 than in the one used for gr.-ser. 2 (p. 426). It has a posterior prolongation (*s. olf*, figs. 49, 50, 59, 65 A, 70 A; pl. 12, fig. 6; pl. 13; figs. 4, 5) tapering backwards, which separates the olfactory canals from one another. This posterior prolongation is continuous dorsally and ventrally with the thin dorsal and ventral parts (s_dio, s_vio) of the interorbital wall. The septum nasi increases considerably in breadth forwards and most anteriorly passes over into the divisio prenasalis communis (*w. pren*, figs. 57 A, 70 A). The lateral face of the septum, which forms the medial face of the nasal cavity, is concave. On its middle ventral part it has a shallow but distinctly marked wide depression, the ventro-medial recess of the nasal cavity (p. 466, *re. vm*, figs. 52 A, 57 B, D, E, 70 A, 71 A; pl. 11, figs. 4, 5; pl. 12, fig. 1), which also extends downwards onto the adjacent part of the solum nasi. Anteriorly and dorsally to this recess a narrow groove, *gr. mn* (figs. 47 B, 52 A, C, 53, 57 A, D, 70 A; pl. 11, fig. 4), extends downwards towards the posterior orifice of the canalis nasobasalis (*c. n-b*; p. 470) though without reaching that orifice In the ventral part of this groove lies the ventral orifice of a narrow ascending canal, *c. ext* (p. 470).

The nasal cavity is bounded posteriorly by the postnasal wall and ventrally to this also to some extent by the anterior end of the pars autopalatina of the palatoquadrate (*ar. aup*, fig. 57 E; p. 456). Besides the posterior face described above (pp. 435—437) the postnasal wall (*w. pn*, figs. 48—51, 59, 65 A, 70 A; pl. 7, fig. 2; pl. 8, figs. 1, 2; pl. 9, fig. 3; pl. 12, figs. 5, 6; pl. 13, figs. 1—3) presents an anterior face and two margins, an upper one, which is directed dorsally-laterally, and a lower one. The anterior face (fig. 51), which forms the posterior face of the nasal cavity, is concave. In the dorso-medial part of this face lies the funnel-like anterior orifice of the canalis olfactorius (*c. olf*). Laterally to the dorsal part of this we find one or two foramina (*c. pr*, *c. mn*, *c. ln*) which are the anterior orifices either of the profundus canal itself (*c. pr*) or of the two branches (*c. mn*, *c. ln*) into which this canal may divide anteriorly (see p. 470). Near the latero-ventral corner of the face is the large foramen (*fe. enp*; see p. 446) which presumably represents the fenestra endonarina posterior. The upper margin of the postnasal wall is strongly convex upwards. Finally, the ventral margin of the postnasal wall extends from the processus postero-ventralis (*pr. pv*, fig. 48) in a medial and somewhat anterior direction to the postero-ventro-medial corner of the ethmoidal region (*co. pm*) and forms the posterior boundary of the fenestra endochoanalis (*fe. ench*). The lateral part of the margin formed by the skeletal bridge (see p. 437) below the probable fenestra endonarina posterior is thick, whereas the medial part, situated antero-ventrally to the medial autopalatine articular area (*art*$_1$*m*), is thin. The latter part is in anterior or posterior aspect somewhat concave and directed ventro-laterally (figs. 49—51).

The lateral nasal wall (figs. 47, 48, 51—53) is thinner than the others. Posteriorly it is continuous with the postnasal wall; dorsally and anteriorly it passes over into the tectum nasi and the prenasal wall. Throughout its length it has a free ventral margin which bounds the fenestra endochoanalis laterally. Its anterior part is pierced by the fenestra endonarina anterior (*fe. ena*) to be described below (p. 446). The shape of the wall is fairly complicated. To facilitate the description it may be regarded as consisting of two divisions, a postero-dorsal one situated behind and above the fenestra endonarina anterior, and a ventral anterior one, the lamina nariochoanalis (*la. nch*), lying ventrally to the fenestra endonarina anterior.

The postero-dorsal division (figs. 47, 48, 51, 52 A, B, 59, 70 A; pl. 8, fig. 1; pl. 9, fig. 3; pl. 11, fig. 5; pl. 12, figs. 1—4) includes a small narrow anterior portion dorsally to the fenestra endonarina anterior, and a posterior portion. The latter is high and comparatively short, thinnest ventrally and increasingly thicker upwards towards its transition into the tectum nasi. It is somewhat arched and in transverse sections its external face is slightly convex and its internal face concave to a corresponding degree. Its external and internal faces are directed laterally and slightly forwards and medially and slightly backwards respectively. It has a free anterior margin, which is the posterior margin of the fenestra endonarina anterior. Its ventral part is curved somewhat medially (*w. lic*, figs. 47 B, C, 48—52, 56, 67 A; pl. 12, fig. 3) and forms the latero-ventral boundary of a shallow recess, the recessus lateralis (*re. l*; see p. 466), of the nasal cavity, situated close dorso-laterally to the posterior part of the fenestra endochoanalis. Posteriorly the division in question passes over into the lateral parts of the postnasal wall. Its ventral margin is, however, bounded off posteriorly from the processus postero-ventralis (*pr. pv*) by a distinct notch (*i. buc*, figs. 47 B, 48) which presumably was developed for the r. buccalis lateralis (see p. 480 and fig. 60).

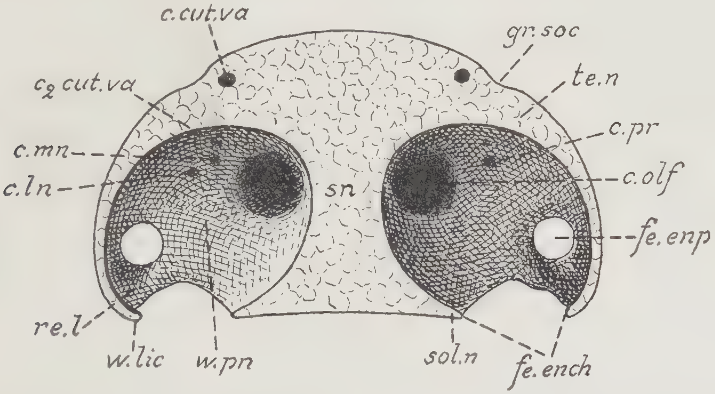


Fig. 51. *Eusthenopteron foordi* Whiteaves. Posterior part of ethmoidal region in anterior view. Restoration based mainly on grinding-series 2. $^3/_1$.

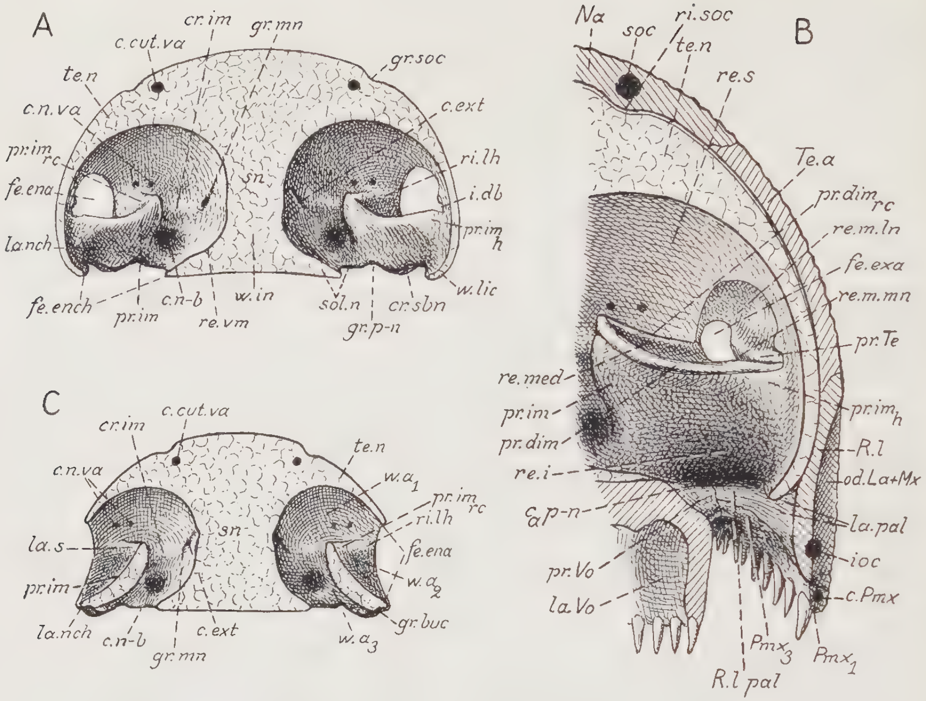
c. cut. va, canal for cutaneous vessel; *c. ln*, canal for r. lateralis narium of n. profundus; *c. mn*, canal for r. medialis narium of n. profundus; *c. olf*, canalis olfactorius; *c. pr*, profundus canal; *$c_2$cut. va*, second branch of canal for cutaneous vessel; *fe. ench*, fenestra endochoanalis; *fe. enp*, opening, probably representing fenestra endonarina posterior; *gr. soc*, groove lodging supraorbital sensory canal ridge; *re. l*, lateral recess of nasal cavity; *sn*. septum nasi; *sol. n*, solum nasi; *te. n*, tectum nasi; *w. lic*, ventral medially curved part of lateral nasal wall; *w. pn*, postnasal wall.

The anterior division of the lateral nasal wall, the lamina nariochoanalis (*la. nch*, figs. 47, 48, 52 A, C, 53, 58, 67 A, 70 A, 71 A, 72 A; pl. 11, figs. 3, 4), consists of two portions, a short posterior one below the incisure *i. db* (fig. 47) in the postero-ventral corner of the fenestra endonarina anterior (see p. 446) and a longer anterior one situated below the large anterior part of the fenestra endonarina anterior. These two portions differ considerably in position and development. The posterior one forms an anterior continuation of the posterior division of the lateral nasal wall and like this has a slightly oblique sagittal position and a most ventral part bent somewhat medially (*w. lic*) and forming part of the lateral boundary of the fenestra endochoanalis. Its dorsal part, which enters into the ventral boundary of the fenestra endonarina anterior, is curved medially, almost at right angles to the main plane of the portion, and thus forms a crest (*pr. im$_h$*, figs. 47, 52 A, B, 70 A) projecting into the nasal cavity. This crest constitutes the posterior horizontal portion of the processus intermedius (*pr. im*) to be described below. It has a dorsal face which is almost horizontal, a ventromedial face, and a small triangular posterior face (fig. 52 A, B). The anterior and larger portion of the lamina nariochoanalis is not mainly sagittal as the posterior one just treated, but may be said to be twisted medially in relation to that portion along an axis through its ventral margin. The degree of twisting is somewhat different anteriorly and posteriorly, but is on the whole about 45°. Owing to the twisting the anterior portion extends far medially into the nasal cavity, where it forms the main part of the processus intermedius. It presents two faces, directed mainly dorso-laterally and ventro-medially respectively. The dorso-lateral face is not plane but curved, so that its anterior part is directed postero-laterally. The anterior part of the face is thus concave in a rostro-caudal direction. The dorso-medial (morphologically dorsal) and ventro-lateral (morphologically ventral) margins are free. The ventro-lateral margin forms the foremost part of the lateral boundary of the fenestra endochoanalis. Anteriorly the lamina nariochoanalis is continuous with the prenasal wall. Its connection with this wall is not at the lateral margin but along an oblique line passing from close above the posterior face of the crista subnasalis (*cr. sbn*; see p. 434) upwards and medially. This oblique anterior connection with the prenasal wall divides the lower part of the posterior face of this wall into a medial and a lateral area, the latter (*w. a$_2$*, fig. 52 C; see p. 445) thus being situated dorso-laterally to the foremost part of the lamina nariochonalis.

As described above the lamina nariochoanalis projects far medially into the nasal cavity and forms a strong process in the anterior lateral part of that cavity. Its medially projecting parts constitute the processus intermedius repeatedly referred to above.

The processus intermedius as thus defined (*pr. im*, *pr. im$_h$*, *pr. im$_{rc}$*, figs. 47, 48, 52, 53, 56, 64 A, 67 A, 70 A, 71 A; pl. 11, figs. 3, 4) is not of a uniform breadth throughout. Anteriorly, approximately at the middle of the anterior half of the nasal cavity, it is produced into a marked angular dorso-medial apex pointing dorsally. It may be regarded as composed of three portions, a posterior horizontal one, a middle main one and an antero-medio-dorsal recurved one. The posterior portion ($pr.\,im_h$), which together with the middle main portion forms the lamina inferior, has been described above. It is fairly narrow. The middle main portion (*pr. im*) increases considerably in breadth forwards. Antero-latero-ventrally it is continuous with the prenasal wall, but antero-medio-dorsally it is bent upward and passes over into the small antero-medio-dorsal recurved portion ($pr.\,im_{rc}$), which extends from the dorso-medial apex of the process in an antero-lateral direction towards the prenasal wall and passes over into a horizontal ridge, the lateral horizontal ridge (*ri. lh*; see below), on the posterior face of that wall. The anterior recurved portion rises fairly much above the middle main portion and is bent somewhat backwards above it. In front of the dorso-medial apex it has a short free upper margin which from the apex runs in an antero-lateral direction and widens antero-laterally so as to present a small dorsal face in its foremost part. Otherwise, it presents two faces, one ventro-latero-posterior, which passes over ventrally into the dorso-lateral face of the middle portion of the processus intermedius, and one small antero-medial, in front of the dorso-medial apex.

The prenasal wall (*w. a*, figs. 47 A, B, 57 B, 59; $w.\,a_1$, $w.\,a_2$, $w.\,a_3$, fig. 52 C; *w. pren*, figs. 71 A, 72 A; cf. also figs. 47 C, 48, 52 A, B, 70 A), formed by the lateral part of the divisio prenasalis communis (*w. pren*, fig. 70 A), is strongly developed. It is highest postero-medially near the foremost part of the septum nasi whence it decreases in height both forwards and laterally. Its upper and lower faces constitute the anterior lateral parts of the upper and lower faces of the ethmoidal region, In addition it has a posterior face, mainly transverse in position. On this face, which forms the anterior face of the nasal cavity, there are two horizontal ridges, one lateral and one medial. The lateral one, the lateral horizontal ridge (*ri. lh*, figs. 52 A, C, 70 A), begins laterally near the lateral margin of the prenasal wall. It increases in height medially and passes over into the anterior recurved portion ($pr.\,im_{rc}$) of the processus intermedius. Together with that it forms an almost horizontal lamina, the lamina superior (*la. s*, figs. 52 C, 67 A, 70 A, 71 A, 72 A), which projects backwards into the nasal cavity. The dorsal face of this lamina has a short medial and a longer postero-lateral margin which converge towards the dorso-medial apex of the processus intermedius, there meeting at an acute angle (see fig. 70 A). The lower face of the lamina is partly made up of the ventro-latero-posteriorly directed face of the overhanging anterior recurved portion of the processus intermedius and passes over both into the foremost upward-bending part of the dorso-lateral face of the middle main portion of the processus intermedius and into the ventro-lateral division ($w.\,a_2$; see below)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pr.im h
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ca p-n
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la.pal
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w.a1
pr.im rc
ri.lh
sn
la.s
fe.ena
pr.im
w.a2
gr.buc
la.nch
c.n-b
c.ext
w.a3
gr.mn

Fig. 52. *Eusthenopteron foordi* Whiteaves. Restorations of the anterior parts of the ethmoidal region in posterior aspect. Particularly the nasal cavities and related structures. The restorations are based mainly on grinding-series 1 and 2. Section areas through cartilage-bone reticulated. *A*, restoration in which the very hindmost part of the ethmoidal region is removed. $^{12}/_{5}$. *B*, right part of the same restoration as in *A*, but with dermal bones. $^{24}/_{5}$. *C*, restoration in which a larger posterior part of the ethmoidal region is removed. $^{12}/_{5}$.

Na, nasal; Pmx_1, Pmx_3, pars dentalis and pars palatina of premaxillary; *R. l*, lateral rostral; *R. l. pal*, processus palatinus of lateral rostral; *Te. a*, anterior tectal; $c_a p$-n, anterior palatonasal canal; *c. cut. va*, canal for cutaneous vessel; *c. ext*, canal for r. externus narium of n. profundus; *c. n-b*, nasobasal canal; *c. n. va*, canals for branches of nerves or vessels; *c. Pmx*, canal for nerve to premaxillary teeth; *cr. im*, crista intermedia; *cr. sbn*, crista subnasalis; *fe. ena*, fenestra endonarina anterior; *fe ench*, fenestra endochoanalis; *fe. exa*, fenestra exonarina anterior; *gr. buc*, groove for r. buccalis lateralis; *gr. mn*, groove for r. medialis narium of n. profundus; *gr. p-n*, groove for r. palatonasalis; *gr. soc*, groove for the ridge *ri. soc*; *i. db*, notch in posterior margin of fenestra endonarina anterior for processes of anterior tectal and lateral rostral extending into nasal cavity; *ioc*, infraorbital sensory canal; *la. nch*, lamina nariochoanalis; *la. pal*, lamina palatina of ethmoidal shield; *la. s*, lamina superior; *la. Vo*, vertical tooth-bearing lamina of vomer; *od. La+Mx*, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *pr. dim*, processus dermintermedius of lateral rostral; $pr.\ dim_{rc}$, anterior recurved portion of processus dermintermedius; *pr. im*, processus intermedius (middle main portion) of lamina nariochoanalis; $pr.\ im_h$, $pr.\ im_{rc}$, posterior horizontal and anterior recurved portions of processus intermedius; *pr. Te*, medial process of anterior tectal; *pr. Vo*, anterolateral process of vomer; *re. i*, *re. med*, recessus inferior and recessus medius of nasal cavity; *re. m. ln*, recess for m. lateralis narium; *re. m. mn*, recess for m. medialis narium; *re. s*, recessus superior of nasal cavity; *re. vm*, ventro-medial recess of nasal cavity; *ri. lh*, lateral horizontal ridge on posterior face of prenasal wall; *ri. soc*, supraorbital sensory canal ridge; *sn*, septum nasi; *soc*, supraorbital sensory canal; *sol. n*, solum nasi; *te. n*, tectum nasi; $w.\ a_1$, $w.\ a_2$, $w.\ a_3$, dorsal, ventro-lateral, and ventro-medial divisions of posterior face of prenasal wall; *w. in*, internasal wall; *w. lic*, ventral medially curved part of lateral nasal wall.

of the posterior face of the prenasal wall. The medial horizontal ridge, the crista intermedia (*cr. im*, figs. 52 A, C, 70 A, 71 A), forms a medial continuation of the lateral horizontal ridge, but is lower and less distinct than that ridge. It extends medially to the nasal septum, terminating just antero-laterally to the ventral orifice of the canal *c. ext* situated in the groove *gr. mn* (p. 439). The lateral horizontal ridge (*ri. lh*) and the crista intermedia (*cr. im*) divide the posterior face of the prenasal wall into a dorsal and a ventral half. The ventral half is in its turn divided by the lamina nariochoanalis into medial and lateral divisions (cf. p. 442). On the posterior face we may thus distinguish three divisions, one dorsal, one ventro-medial and one ventro-lateral (fig. 52 C). The dorsal division ($w. a_1$) which comprises about one half of the entire face, is broad, concave and directed on the whole straight backwards. It has no distinct boundaries towards the adjacent parts of the ventral face of the tectum nasi and the lateral face of the septum nasi. On it are found the posterior orifices of two narrow canals (*c. n. va*, fig. 52 A, C; see pp. 470—471). The ventro-medial division ($w. a_3$), which also on the whole faces straight backwards, is comparatively narrow, but broader dorsally than ventrally. It is bounded laterally by the processus intermedius, whereas medially and ventrally it passes over into the lateral face of the septum nasi and the dorsal face of the solum nasi. In its lower part is found a wide foramen which forms the posterior orifice of the canalis nasobasalis (*c. n-b*; p. 470). Finally, the ventro-lateral division ($w. a_2$) has the shape of a triangle pointing downwards. This division faces backwards and somewhat downwards except in its most ventral part which constitutes the straight backward directed posterior face of the crista subnasalis. It passes over ventro-medially into the dorso-lateral face of the processus intermedius (lamina nariochoanalis) in such a way that a groove is formed between it and that face (fig. 47 B). This groove continues in a postero-dorso-medial direction between the middle main and anterior recurved portions of the processus intermedius to the dorso-medial apex of that process and thus leads from close behind the crista subnasalis backwards, upwards and medially into the nasal cavity.

The tectum nasi (*te. n*, figs. 47, 51—53, 71 A; pl. 11, figs. 3—6; pl. 12, figs. 1—3) is thick medially at its transition into the septum nasi, but decreases in thickness laterally. It passes over anteriorly into the prenasal wall, posteriorly into the postnasal wall and laterally into the postero-dorsal division of the lateral nasal wall. Its lower face shows a small foramen posteriorly, which is the ventral orifice of a narrow canal (c_2*cut. va*, figs. 51, 57 A, C, E; p. 469).

The solum nasi (*sol. n*, figs. 47 C, 48, 51, 52 A, 53; pl. 9, fig. 3; pl.

11, fig. 5; pl. 12, figs. 1, 2), which to a large extent is occupied by the fenestra endochoanalis (pp. 447—448), is represented by antero-medial and medial parts only and forms a strong, almost horizontal ledge stretching from the ventro-medial part of the prenasal wall backwards along the septum nasi. It has a free margin which bounds the fenestra endochoanalis antero-medially and medially and terminates posteriorly at the postero-ventro-medial corner (*co. pm*, fig. 48) of the ethmoidal region, where it meets the lateral margin of the anterior suborbital ledge (*sh. sbo*) almost at right angles. As already mentioned (p. 439), the ventro-medial recess of the nasal cavity (*re. vm*) extends from the lateral face of the septum nasi downwards onto the dorsal face of the solum nasi.

The fenestra endonarina anterior (*fe. ena*, figs. 47, 52 A, C, 53; pl. 11, fig. 3) is a comparatively large opening in the anterior part of the lateral nasal wall. It is directed laterally and somewhat upwards and forwards. Its anterior, dorsal and posterior boundary is formed by a continuous concave margin of the prenasal and lateral nasal walls, its ventral boundary by the lamina nariochoanalis. Owing to the anterior portion of the lamina nariochoanalis being twisted medially, the anterior part of the fenestra extends downwards to the ventro-lateral margin of the said lamina. In the postero-ventral corner of the fenestra is a distinct notch, *i. db* (figs. 47, 52 A), with thickened margins forming a support for processes of dermal bones (*pr. dim*, *pr. Te*, figs. 52 B, 53) which extend inwards into the nasal cavity and fill the notch completely.

The fenestra endonarina posterior is probably represented by the large opening (*fe. enp*, figs. 48—51, 57 A, E, 65 A; pl. 8, fig. 2; pl. 13, fig. 1) perforating the ventro-lateral part of the postnasal wall that has been repeatedly mentioned above. This opening is much wider than was necessary for the nerves and vessels which may be assumed to have traversed it (cf. p. 477). It leads backwards to the orbit from the postero-lateral part of the nasal cavity and is situated straight behind the part of the nasal cavity that lies immediately inside the fenestra exonarina anterior (*fe. exa*, figs. 52 B, 57 C). As has been pointed out above (p. 436), it opens into a funnel-like depression in the posterior face of the postnasal wall. On the lateral side of the funnel-like depression a short, broad and shallow groove, *gr. ntp* (figs. 48—50; pl. 13, fig. 3), goes backwards and somewhat laterally. A posterior external nasal tube (nasolachrymal duct) was probably developed (cf. pp. 512—513) and as there is no other opening through which it could have left the nasal cavity, we are forced to the conclusion that this tube had its passage backwards through the large opening (*fe. enp*) in the postnasal wall. From that opening it must have passed backwards to the orbital opening

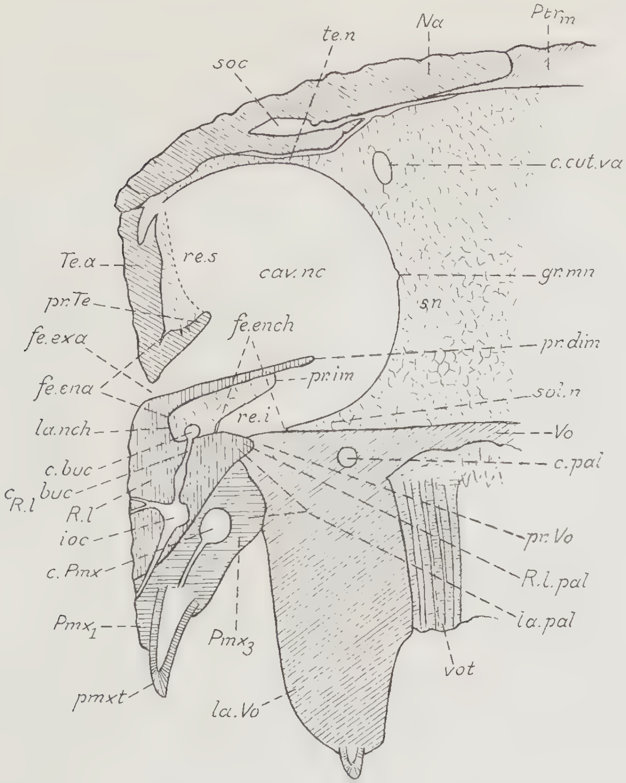


Fig. 53. *Eusthenopteron foordi* Whiteaves. Diagrammatic transverse section of the nasal capsule of left side through the posterior part of the fenestra exonarina anterior. Combined from drawings Nos. 34—41 of grinding-series 1. Posterior view. $^7/_1$.

Na, nasal; *Pmx_1, Pmx_3,* pars dentalis and pars palatina of premaxillary; *Ptr_m,* posterior median postrostral; *R. l,* lateral rostral; *R. l. pal,* processus palatinus of lateral rostral; *Te. a,* anterior tectal; *Vo,* vomer; *cav. nc,* nasal cavity; *c. buc,* canal for r. buccalis lateralis; *c. cut. va,* canal for cutaneous vessel; *c. pal,* palatine canal; *c. Pmx,* canal for nerve to premaxillary teeth; *$c_{R.l}buc$,* canal for branch of r. buccalis lateralis to canal organ in lateral rostral; *fe. ena,* fenestra endonarina anterior; *fe. ench,* fenestra endochoanalis; *fe. exa,* fenestra exonarina anterior; *gr. mn,* groove for r. medialis narium of n. profundus; *ioc,* infraorbital sensory canal; *la. nch,* lamina nariochoanalis; *la. pal,* lamina palatina of ethmoidal shield; *la. Vo,* vertical tooth-bearing lamina of vomer; *pmxt,* premaxillary tooth; *pr. dim,* processus dermintermedius of lateral rostral; *pr. im,* processus intermedius of lamina nariochoanalis; *pr. Te,* process of anterior tectal extending into nasal cavity; *pr. Vo,* antero-lateral process of vomer; *re. i, re. s,* recessi inferior and superior of nasal cavity; *sn,* septum nasi; *soc,* supraorbital sensory canal; *sol. n,* solum nasi; *te. n,* tectum nasi; *vot,* vomerine tusk.

in the groove *gr. ntp* and behind this immediately medially to the dermal bones forming the lateral wall of the foremost part of the orbit (see fig. 55).

The fenestra endochoanalis (*fe. ench,* figs. 47 C, 48, 51, 52 A, 53, 56, 57 B, 64 A, 70 A; pl. 8, fig. 1; pl. 9, fig. 3; pl. 11, figs. 4, 5; pl. 12, fig. 3) is a large opening occupying the latero-posterior part of the solum nasi. It is bounded anteriorly by a transverse edge on the lower side of the lamina nariochoanalis and by the antero-medial part of the solum nasi, medially by the medial part of the solum nasi, posteriorly by the free ventral margin of the postnasal wall, laterally partly by the ventral medially curved parts (*w. lic*) of the posterior division of the lateral nasal wall and of the posterior portion of the lamina nariochoanalis, and partly by the ventro-lateral margin of the anterior portion of the lamina nariochoanalis.

Before entering upon the fenestra exonarina anterior, the fenestra exochoanalis, the fossa apicalis and the cavities and canals of the snout we must treat certain of the dermal bones of the ethmoidal region and the foremost part of the palatoquadrate with its dermal bones.

The general disposition of the numerous bones composing the ethmoidal shield has been described in a special chapter above (pp. 346—352). On the outside of the postero-ventro-lateral corner of this shield is a comparatively large unornamented area (*od. La + Mx*, figs. 34, 50, 52 B, 58 A, 68 A; pl. 6, fig. 2; pl. 7, figs. 1, 2; pl. 9, fig. 1; pl. 10; pl. 12, figs. 4, 6; pl. 13, fig. 2). This area is developed on parts of the premaxillary, lateral rostral, and posterior tectal (supraorbito-tectal) and sometimes extends also onto the postero-lateral corner of the anterior tectal. It was overlapped by the lachrymal (*La*) and the maxillary (*Mx*, figs. 64 A, 68 A; cf. *od. Mx*, fig. 68 E). In the antero-ventral part of the area lies the posterior opening (*ioc*, figs. 34, 52 B, 68 A, 86 A; pl. 6, fig. 2; pl. 7, fig. 1; pl. 9, fig. 1; pl. 10) of the part of the infraorbital sensory canal that is enclosed in the lateral rostral. Ventrally to this opening there is another smaller one, which is the posterior orifice of a canal (p. 474; *c. Pmx*, figs. 52 B, 68 A) piercing the premaxillary.

Of the various bones of the ethmoidal shield only the anterior tectal, the lateral rostral and the palatal lamina of the ethmoidal shield will be treated here.

The anterior tectal (*Te. a*, figs. 34, 52 B, 53, 58, 68 A; pl. 6, figs. 1, 2; pl. 7, figs. 1, 2; pl. 9, figs. 1, 4; pl. 10; pl. 11, fig. 4) lies in the main on the outside of the ethmoidal region but has also a medial process which extends medially into the nasal cavity. The main external part of the bone, the facial part, which is ornamented on its outside, covers the dorsal part of the fenestra endonarina anterior and forms the dorsal margin of the fenestra exonarina anterior. The medial process (*pr. Te*, figs. 52 B, 53, 58 A; pl. 6, fig. 1; pl. 9, fig. 1; pl. 11, fig. 4; pl. 12, figs. 1, 2), which issues from the lowermost posterior part of the bone, has a fairly small extent both in rostro-caudal and transverse directions. It extends inwards through and occupies the dorsal part of the notch *i. db* (fig. 47 B) in the postero-ventral corner of the fenestra endonarina anterior, but goes a little medially to that notch and thus projects into the nasal cavity. Most posteriorly, behind the fenestra exonarina anterior, it rests on the hindmost part of the processus dermintermedius (*pr. dim*) of the lateral rostral described below. Anteriorly and medially it rises gradually from the processus dermintermedius so that a small recess of the nasal cavity (cf. p. 465), widening medially and anteriorly, is formed between it and the last-mentioned process. This recess (*re. m. mn*, figs. 52 B, 57 A—C, 58 A; pl. 12, fig. 1) is bounded by dermal bones exclusively and is situated immediately behind the fenestra exonarina anterior. It was possibly the place of origin of a nasal muscle corresponding to the m. medialis narium of the frog (see pp. 539—540). The portion of the facial part of the anterior tectal that covers the dorsal part of the fenestra endonarina anterior has on its medial face a fairly broad depression which extends backwards dorsally to the medial process. This depression (*re. m. ln*, figs. 52 B, 57 A, C, D; pl. 6, fig. 1; pl. 7, fig. 1; pl. 11, fig. 6; pl. 12, fig. 1) forms a recess of the nasal cavity, bounded dorsally by the dorsal margin of the fenestra endonarina anterior. It seems to have served as a place of origin of a muscle corresponding to the m. lateralis narium of the frog (see p. 539).

The lateral rostral (*R. l*, *pr. dim*, $pr.\,dim_{rc}$, *R. l. pal*, figs. 34, 52 B, 53, 56, 58, 68 A, 70 A, 71 A, 72 A, 86 A; pl. 6, figs. 1, 2; pl. 7, figs. 1, 2; pl. 8, fig. 3; pl. 9, figs. 1—4; pl. 10; pl. 11, figs. 3—6; pl. 12, figs. 1—3) consists of a pars facialis and two medial processes, a dorsal one, the processus dermintermedius, and a ventral one, the processus palatinus. The pars facialis covers the external side of the ventral part of the lateral nasal wall and forms the ventral margin of the fenestra exonarina anterior. The processus dermintermedius (*pr. dim*, $pr.\,dim_{rc}$) is large and broad. It extends from the dorsal margin of the facial part inwards through the lowermost part of the fenestra endonarina anterior, over the whole upper margin of the lamina nariochoanalis and over and somewhat beyond (figs. 53, 56, 70 A) the whole upper face of the processus intermedius. It is curved in the same way as the upper face of the processus intermedius and like that process it may therefore be regarded as composed of three portions, a posterior horizontal, a middle main, and an antero-medio-dorsal recurved portion. The posterior horizontal portion is in contact with the lower face of the medial process (*pr. Te*) of the anterior tectal most postero-laterally in the notch *i. db* of the fenestra endonarina anterior, whereas further forwards and medially it forms the floor of the recess *re. m. mn* described above. The foremost part of the main portion is curved upward and covers not only the middle main portion of the processus intermedius, but also the ventro-lateral division ($w.a_2$, fig. 52 C) of the posterior face of the prenasal wall. The recurved portion ($pr.dim_{rc}$, figs. 52 B, 58 A, 68 A, 70 A, 71 A, 72 A) forms the continuation of the upward-bent part of the middle main portion and covers the lower side of the lamina superior (*la.s*; see p. 443 above). In certain specimens its lateral part continues upwards and forwards and completely covers the lateral part of the lamina superior (fig. 72 A) formed by the lateral horizontal ridge of the prenasal wall. The processus palatinus of the bone (*R.l.pal*, see especially figs. 53, 58 B, 71 A, 86 A) extends medially underneath the anterior part of the lamina nariochoanalis and the adjacent part of the prenasal wall and also underneath an anterior part of the fenestra endochoanalis. It enters into the formation of the palatal lamina of the ethmoidal shield.

The palatal lamina of the ethmoidal shield (*la.pal*, figs. 52 B, 53, 56, 58; pl. 8, fig. 1; pl. 9, fig. 4; pl. 11, fig. 2) is a comparatively thick ledge which covers a marginal zone of the lower face of the ethmoidal region and an antero-lateral part of the fenestra endochoanalis of either side. It is a double formation throughout, being formed by the palatal parts of the premaxillaries proper (Pmx_1) below and by the palatal processes of the lateral and medial rostrals above (*R.l.pal*, *R.m.pal*, figs. 53, 56, 58 B). In the majority of the specimens examined the medial rostral and premaxillary are fused with one another and with the foremost element of the nasal series to form a compound naso-rostro-premaxillary (see p. 347); in these specimens the palatal parts are also fused (NRP_3, $ri.NRP_3$, figs 56, 68 D, 72 A, 87 A; pl. 9, fig. 1; pl. 11, figs. 1, 2, 6). Along its palatal margin the palatal lamina shows a median unpaired and a lateral paired process. The median unpaired process ($pr_m NRP_3$, figs. 56, 64 A, 87 A; pl. 8, fig. 1), which is obtuse with a rounded contour and directed straight backwards, divides the anterior palatal fenestra (*fe.pal*) very incompletely into right and left halves. The lateral paired process ($pr_l NRP_3$), which is directed postero-medially, is connected by a long suture (*sut.Vo*, fig. 68 D) with an antero-lateral process (*pr.Vo*; p. 451) of the vomer. Both the lateral process of the palatal lamina and the antero-lateral process of the vomer are thickened and thus form a broad, somewhat ridge-like part connecting the ethmoidal shield with the vomer and separating the fenestra exochoanalis (*fe.exch*) from the fossa apicalis (*fo.ap*; p. 458).

The vomer (*Vo*, *la.Vo*, *pr.Vo*, $pr_p Vo$, *sh.Vo*, figs. 50, 52 B, 53, 55, 56, 58, 60, 64 A, 65 A, 87 A; pl. 6, fig. 1; pl. 8; pl. 9, figs. 2—4; pl. 11, figs. 2—6; pls. 12, 13; cf. JARVIK 1937, pp. 84—86, 105—108) is a triangular plate with a high vertical tooth-bearing lamina on its ventral side. It is produced backwards along the parasphenoid into a pointed posterior process ($pr_p Vo$) and covers a large part of the lower face of the ethmoidal region, an anterior and medial part of the fenestra endochoanalis, and a small antero-lateral part of the lower face of the interorbital wall. Its anterior margin is transverse and forms the posterior boundary of the anterior palatal fenestra (*fe. pal*). Its antero-lateral part is developed as a broad and short process (*pr. Vo*, figs. 52 B, 53, 56) which, as mentioned above, has a long sutural connection with the lateral process ($pr_l NRP_3$) of the palatal lamina of the ethmoidal shield. Postero-medially to the fenestra endochoanalis the bone extends somewhat postero-laterally beyond the lower face of the endocranium and in this part it thus forms a ledge below the endocranium, the vomerine shelf (*sh. Vo*, figs. 50, 56), on which is situated a part of the pit *fo. cr. vm* described above (p. 437).

The vertical lamina (*la. Vo*, figs. 50, 52 B, 53, 56, 58, 64 A, 87 A), which bears two rows of teeth (vt_e, vt_i) on its ventral margin, descends from the bone some distance behind its anterior end. It is arched in such a way that two parts can be distinguished, an anterior and medial transverse part and a posterior and lateral mainly rostro-caudal part, the former of which enters into the posterior boundary of the fossa apicalis (p. 451), whereas the latter is situated close medially and ventrally to the fenestra exochoanalis. Close postero-medially to the tooth-bearing lamina are two large tusks (*vot*, figs. 50, 53, 56, 58 B, 87 A; pl. 6, fig. 1; pl. 8; pl. 11, fig. 4; pl. 12, figs. 1, 2; vot_1, vot_2, pl. 9, fig. 4) one of which, however, is generally missing, leaving only a wide pit (*fo. vot*) at the side of the remaining one.

The pars autopalatina of the palatoquadrate (*Aup*, figs. 54, 55, 64 A, 65 A, 70 A; pl. 10; pl. 12, figs. 4—6; pl. 13) is ossified and forms the anterior part of the single large palatoquadrate ossification (see p. 429). Like the posterior parts of the palatoquadrate it is arched so that its external (dorsal) side is concave and its internal (ventral) side convex in transverse sections. It is delicate posteriorly where it may be perforated by fenestrations (*fe. pq*), but increases considerably in thickness forwards. Though narrowing forwards it is nevertheless comparatively broad throughout and terminates anteriorly with a rounded tip at which it is provided with a postero-dorsal process, the processus apicalis (*pr. ap*). The external (dorsal) face is traversed by a low, almost transverse ridge (*ri. lev*) into which a part (portio principalis, see p. 525) of the m. levator bulbi was probably inserted. Both the lateral and the medial marginal parts of the pars autopalatina are curved upward so that a dorso-lateral and a dorso-medial margin may be distinguished, the dorso-medial one being situated more dorsally than the dorso-lateral one (fig. 55). These two margins converge forward but are separated an-

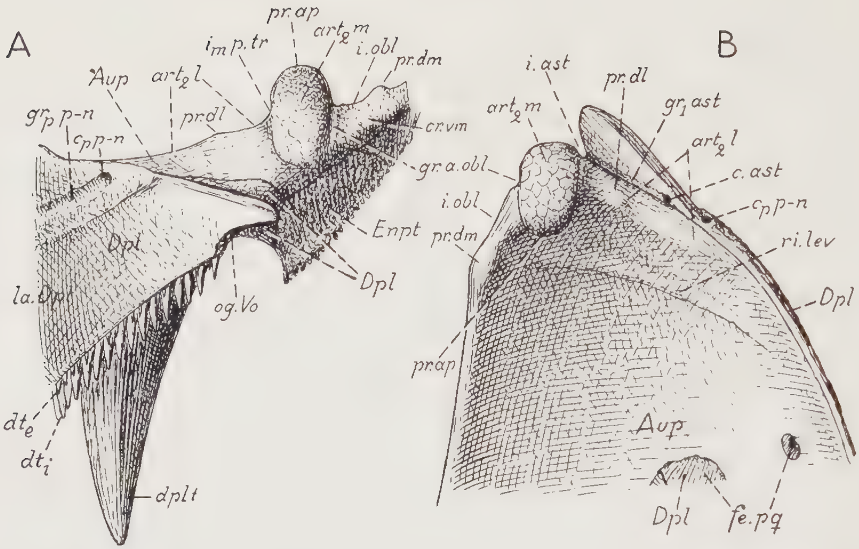


Fig. 54. *Eusthenopteron foordi* Whiteaves. The pars autopalatina of the right palatoquadrate with anterior parts of the dermopalatine and entopterygoid attached. *A*, anterior, *B*, dorsal view. Restoratios based on several specimens. $^4/_1$.

Aup, pars autopalatina of palatoquadrate; *Dpl*, dermopalatine; *Enpt*, entopterygoid; art_2l, art_2m, lateral and medial ethmoidal articular areas; *c. ast*, canal for postchoanal nerve anastomosis; *cr. vm*, ventro-medial crest of pars autopalatina; $c_pp\text{-}n$, posterior palatonasal canal; *dplt*, dermopalatine tusk; dt_e, dt_i, external and internal rows of teeth of tooth-bearing lamina of dermopalatine; *fe. pq*, irregular fenestrations in palatoquadrate; *gr. a. obl*, groove, probably for branch of a. palatina supplying m. obliquus inferior; $gr_pp\text{-}n$, posterior groove for r. palatonasalis; gr_1ast, groove for postchoanal nerve anastomosis on dorsal face of dermopalatine; *i. ast*, notch in medial margin of dermopalatine for postchoanal nerve anastomosis; $i_mp.\,tr$, notch forming medial wall of pit, probably for insertion of portio transversalis of m. levator bulbi; *i. obl*, notch for oblique eye muscles; *la. Dpl*, lateral vertical tooth-bearing lamina of dermopalatine; *og. Vo*, area of dermopalatine, overlapping vomer; *pr. ap*, processus apicalis of pars autopalatina; *pr. dl*, *pr. dm*, dorso-lateral and dorso-medial processes of pars autopalatina; *ri. lev*, ridge for insertion of principal portion of m. levator bulbi.

teriorly by the processus apicalis. Immediately behind this process the dorso-medial margin has a shallow wide notch, *i. obl*, bounded posteriorly by a small elevation, the dorso-medial process (*pr. dm*). Ventrally to the shallow notch lies a low crest, strongly convex in transverse sections, the ventro-medial crest (*cr. vm*, fig. 54), which is separated anteriorly from the processus apicalis by a narrow vertical groove, *gr. a. obl*, and which extends in a posterior direction to about opposite the dorso-medial process. On the antero-dorsal face of the processus apicalis and ventrally to this there is a very distinct articular area, the medial ethmoidal articular area (art_2m), which is higher than broad and devoid of periostal bone. Immediately laterally to the processus apicalis is a short rostro-caudal groove or notch open laterally

($i_{m}p.\ tr$). Postero-laterally to this groove the dorso-lateral margin is thickened and bears a distinct articular facet, the lateral ethmoidal articular area (art_2l). This facet is composed of an antero-medial part facing dorsally and a postero-lateral part facing dorsally and somewhat antero-laterally. These two parts are separated by a slight elevation, the dorso-lateral process (*pr. dl*).

The dermal bones related to the pars autopalatina are the dermopalatine and the entopterygoid (*Enpt*, figs. 54 A, 55, 56, 64 A, 65 A, 87 A; pl. 8, fig. 1; pl. 13, figs. 3—5). These two bones cover the lower face of the pars autopalatina except for the very foremost part and a narrow area along the dorso-medial margin.

The dermopalatine (*Dpl*, *la. Dpl*, figs. 54—56, 64 A, 65 A, 87 A; pl. 8, fig. 1; pl. 10; pl. 12, figs. 3—6; pl. 13) is composed of two laminae, one medial and horizontal and one lateral and vertical. The medial horizontal lamina lies entirely on the ventral (internal) side of the palatoquadrate. The lateral lamina (*la. Dpl*), which is high and whose ventral margin is tooth-bearing, is attached to the medial one somewhat above the middle of its height, and its dorsal part thus forms a high sharp edge, the dorso-lateral crest. This crest covers the upward-curved lateral marginal part of the pars autopalatina as far forwards as the postero-lateral end of the lateral ethmoidal articular area (art_2l), but continues forwards beyond that to the very tip of the anterior projecting part of the dermopalatine, where, however, it gradually becomes lower and broader (fig. 54). This foremost part of the crest is separated from the pars autopalatina by an interspace widening forwards. At the posterior end of this interspace and on the medial face of the crest lies the anterior orifice of a canal, *c. ast* (p. 472), for the postchoanal nerve anastomosis. This canal is continued by a shallow groove, gr_1ast (fig. 54 B), running at the bottom of the interspace in an antero-medial and somewhat ventral direction to the most anterior part of the medial margin of the horizontal lamina of the dermopalatine, just antero-ventrally to the antero-medial end of the lateral ethmoidal articular area (art_2l) and on a level with the ventral (internal) face of the pars autopalatina. At this place the groove in question curves downwards, causing a deep narrow notch, *i. ast* (figs. 54 B, 56), in the medial margin of the horizontal lamina. From the lower end of this notch a short groove, gr_2ast (fig. 56) runs backwards and somewhat medially on the lower side of the horizontal lamina. On the lower side of the free anterior tip of the dermopalatine is a much depressed and rough area (*og. Vo*, figs. 54 A, 56) overlapping the vomer. The lateral face of the lateral tooth-bearing lamina of the dermopalatine is practically sagittal posteriorly, but anteriorly it is directed antero-laterally and somewhat dorsally. The posterior part of the face, to which are attached the lachrymal (*La*, fig. 55) and the maxillary (*Mx*), is rough in appearance and generally shows a distinct longitudinal groove ($gr_{p}p\text{-}n$, fig. 54 A) the anterior end of which lies at the very dorsal edge of the dorso-lateral crest of the dermopalatine not very far postero-dorso-laterally to the anterior orifice of the canal (*c. ast*) for the postchoanal nerve anastomosis. This groove ($gr_{p}p\text{-}n$) first goes downwards and backwards and then in its hinder part, not shown in fig. 54, backwards and upwards, terminating posteriorly at the very dorsal edge of the hindmost part of the dorso-lateral crest close to the ectopterygoid (cf. *Ecpt*, fig. 87 A.) The groove is covered by the dermal bones of the cheek so that a canal, the posterior palatonasal canal ($c_{p}p\text{-}n$, fig. 65 A), is formed. The foremost dorsal part of this canal may in certain individuals be completely enclosed in the lateral lamina of the dermopalatine (fig. 54 A, B). The anterior parts of the lachrymal and maxillary are not attached to the dermopalatine but are separated from that by an interspace widening anteriorly. In this connection it may also be mentioned that the anterior part of the maxillary is provided with a dorsal process pointing somewhat anteriorly (*pr. Mx*, fig. 68 A; pl. 13, fig. 1) with a concave anterior and a slightly convex postero-dorsal margin. The upper part of this process is bent medially and terminates with a somewhat thickened tip close to the dorso-lateral crest of the dermopalatine slightly postero-laterally to the anterior orifice of the canal (*c. ast*) for the postchoanal nerve anastomosis.

The lower part of the lateral, vertical and tooth-bearing lamina of the dermopalatine lies in the posterior continuation of the ventral tooth-bearing lamina of the vomer (*la. Vo*) and is provided with two rows of small teeth (dt_e, dt_i, figs. 54 A, 55, 56) similar to those of that lamina. The horizontal lamina of the dermopalatine bears two large tusks (*dplt*, figs. 54 A, 55, 56, 87 A; pl. 13, fig. 5) of a similar size as the vomerine tusks. However, as is the case with the vomerine tusks, one of them is generally absent and represented by its basal pit only (*fo. dplt*). The dentition of the ectopterygoid (*Ecpt*, fig. 87 A) is fundamentally as that of the dermopalatine, the ectopterygoid being also provided with a lateral vertical tooth-bearing lamina and a medial horizontal lamina equipped with large tusks. These are, however, four in number and disposed in pairs. The foremost of them ($ecptt_1$) is shown in fig. 87 A.

As is clearly shown by grinding-series 2, the pars autopalatina and the dermal bones developed in relation to it (the anterior part of the palatoquadrate-cheek complex) are attached to the endocranium and its dermal bones (the anterior part of the divisio cranialis anterior) in the following way (figs. 50, 54—56, 64 A, 65 A, 70 A). The part of the dorso-medial margin of the pars autopalatina that is situated behind the

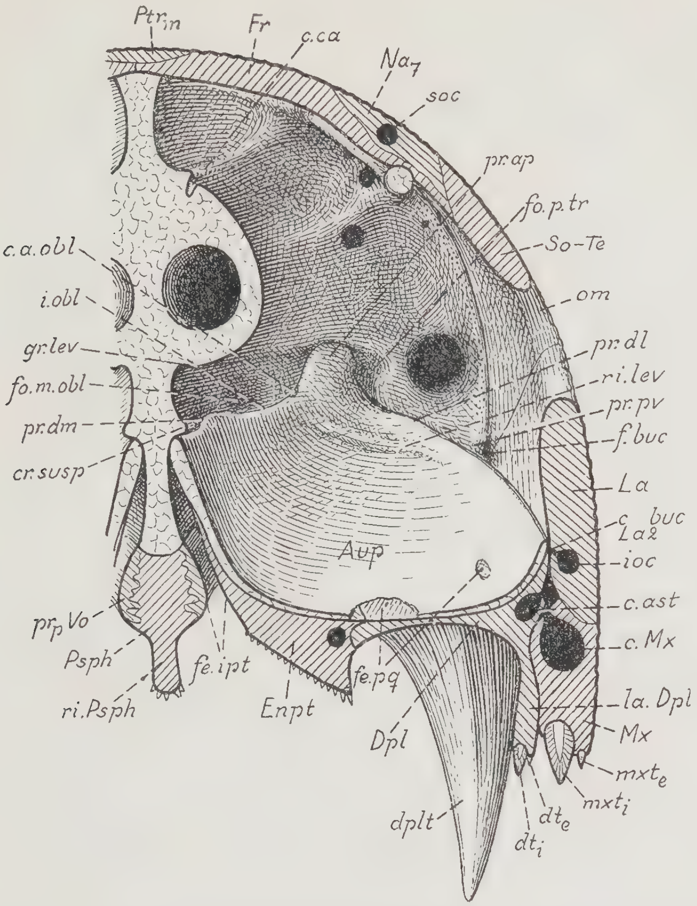


Fig. 55. *Eusthenopteron foordi* Whiteaves. Right half of the anterior part of the divisio cranialis anterior and the palatoquadrate-cheek complex in posterior view. Restoration based on grinding-series 2 and on several specimens. $^4/_1$.

Aup, pars autopalatina of palatoquadrate; *Dpl,* dermopalatine (medial horizontal lamina); *Enpt,* entopterygoid; *Fr,* frontal; *La,* lachrymal; *Mx,* maxillary; Na_7, nasal 7; *Psph,* parasphenoid; Ptr_m, posterior median postrostral; *So-Te,* supraorbito-tectal; *c. a. obl,* canal, probably for branch of a. palatina supplying m. obliquus inferior; *c. ast,* canal for post-choanal nerve anastomosis; *c. ca,* canal for v. cerebralis anterior; $c_{La2}buc$, canal for branch of r. buccalis lateralis supplying canal organ in lachrymal; *c. Mx,* canal in maxillary for nerve supplying maxillary teeth; *cr. susp,* crista suspendens; *dplt,* dermopalatine tusk; dt_e, dt_i, external and internal rows of teeth on tooth-bearing lamina of dermopalatine; *f. buc,* foramen for r. buccalis lateralis; *fe. ipt,* interpterygoid fenestra; *fe. pq,* irregular fenestrations in palatoquadrate; *fo. m. obl,* pit for origin of oblique eye muscles; *fo. p. tr,* pit for insertion of pórtio transversalis of m. levator bulbi; *gr. lev,* groove for origin of principal portion of m. levator bulbi; *i. obl,* notch for oblique eye muscles; *ioc,* infraorbital sensory canal; *la. Dpl,* vertical tooth-bearing lamina of dermopalatine; mxt_e, mxt_i, external and internal rows of maxillary teeth; *om,* margin of orbital opening; *pr. ap,* processus apicalis of pars autopalatina; *pr. dl, pr. dm,* dorso-lateral and dorso-medial processes of pars autopalatina; *pr. pv,* postero-ventral process of ethmoidal region; $pr_p Vo$, posterior process of vomer; *ri. lev,* ridge for insertion of principal portion of m. levator bulbi; *ri. Psph,* tooth-bearing ridge of parasphenoid; *soc,* supraorbital sensory canal.

dorso-medial process (*pr. dm*) is in contact with the lower side of the crista suspendens (*cr. susp*). The dorso-medial process itself fits into the pit *fo. pr. dm* immediately in front of the crista suspendens. The notch *i. obl* in the dorso-medial margin of the pars autopalatina lies immediately ventro-laterally to the pit *fo. m. obl* in the endocranium and was presumably caused by the oblique muscles of the eye, which may be assumed to have had their origin in the pit *fo. m. obl.* The ventro-medial crest (*cr. vm*) rests in the pit *fo. cr. vm* on the ventro-medial part of the posterior face of the ethmoidal region and on the upper face of the vomerine shelf (*sh. Vo*). The medial ethmoidal articular area (art_2m) of the pars autopalatina is of exactly the same size and shape as the medial autopalatine articular area (art_1m) of the postnasal wall, and these two areas, both of which are devoid of periostal bone, thus match one another completely. The dorsal point of the processus apicalis (*pr. ap*), which is directed backwards, abuts against the high dorso-posterior margin of the medial autopalatine articular area (art_1m) and thus prevents the palatoquadrate from sliding backwards. The notch $i_mp.\,tr$ in the pars autopalatina has such a position opposite the notch $i_lp.\,tr$ in the posterior face of the postnasal wall that together they form a comparatively deep and narrow pit (*fo. p. tr*, figs. 55, 65 A), opening posteriorly, into which a portion (the portio transversalis; cf. p. 524) of the m. levator bulbi seems to have been inserted. The lateral ethmoidal articular area (art_2l) of the autopalatine closely matches the lateral autopalatine articular area (art_1l) of the postnasal wall and these two areas are in close contact with one another. The dorso-lateral process (*pr. dl*) of the pars autopalatina abuts against the medial side of the postero-ventral process (*pr. pv*) of the ethmoidal region. The part of the pars autopalatina bearing the lateral ethmoidal articular area occupies such a position ventrally to the ethmoidal region that it enters into the posterior boundary of the nasal cavity and supplements the postnasal wall ventrally (cf. fig. 57 E, *ar. aup*). The thickened extremity of the antero-dorsal process (*pr. Mx*; see p. 454) of the maxillary may possibly be in contact with the lateral side of the postero-ventral process of the ethmoidal region and at any rate it lies very close to that process. The anterior free part of the dermopalatine extends forwards underneath the ethmoidal region, covers the postero-medial part of the fenestra endochoanalis, and forms the postero-medial margin of the fenestra exochoanalis. The foremost end of the dermopalatine overlaps the dorsal face of the vomer, and judging from the rough appearance of its overlapping area (*og. Vo*) its connection with that bone must have been intimate and probably rigid (see pl. 12, fig. 3). The descending tooth-bearing lamina of the vomer (*la. Vo*) and the lower tooth-bearing parts of the lateral vertical laminae of the dermopalatine (*la. Dpl*) and ectopterygoid (*la. Ecpt*, fig. 87 A) form together a long tooth-bearing crest in the roof of the mouth. Finally the anterior ends of the lachrymal and maxillary overlap the unornamented area (*od. La + Mx*, figs. 52 B, 68 A; cf. fig. 65 A) on the outside of the postero-ventro-lateral corner of the ethmoidal shield.

As may be readily understood from the above, the endocranium is in almost continuous contact with the pars autopalatina of the palatoquadrate from the posterior end of the crista suspendens forwards and laterally as far as the postero-ventral process at the ventro-lateral corner of the postnasal wall. No less than six or possibly even seven connections may be distinguished between the anterior parts of the palatoquadrate-cheek complex and the divisio cranialis anterior. Three or possibly four of these connections are developed so as to prevent the palatoquadrate-cheek complex from moving upwards and to a large extent also so as to stop movements in transverse and rostro-caudal directions. These connections are as follows: 1) The connection between the crista suspendens (*cr. susp*) and the pit *fo. pr. dm* of the endocranium and the dorso-medial margin and dorso-medial process (*pr. dm*) of the pars autopalatina; 2) the connection between the medial autopalatine articular area (art_1m) of the postnasal wall and the medial ethmoidal articular area (art_2m) of the pars autopalatina; 3) the connection between the lateral autopalatine articular area (art_1l) of the postnasal wall and the lateral ethmoidal articular area (art_2l) of the pars autopalatina; and 4) the possible connection between the postero-ventral process (*pr. pv*) of the ethmoidal region and the extremity of the antero-dorsal process (*pr. Mx*) of the maxillary (the actual existence of this connection could not be established with certainty). The remaining three connections — 5) the connection between the pit *fo. cr. vm* on the endocranium and vomer and the ventro medial crest (*cr. vm*) of the pars autopalatina; 6) the connection between the upper side of the vomer and the rough anterior area *og. Vo* of the dermopalatine; and 7) the connection between the unornamented postero-dorso-ventral corner (*od. La + Mx*) of the ethmoidal shield and the lachrymal and maxillary — prevent movements of the palatoquadrate in a downward direction, but also to a large extent in transverse directions. These six or seven connections show beyond doubt that the palatoquadrate-cheek complex was quite immovable in relation to the divisio cranialis anterior. The opinion earlier advanced by the writer (Jarvik 1937, pp. 112—117) that the palatoquadrate in *Eusthenopteron* was rigidly attached to the endocranium is thus confirmed by the present investigation. The medial autopalatine and the medial ethmoidal articular areas (art_1m, art_2m), which are devoid of periostal bone, lie a little apart in grinding-series 2 (pl. 12, fig. 6; pl. 13, figs. 1, 2). It is not impossible that the interspace between them was occupied by cartilage and that, as previously supposed by the present writer, this cartilage formed a synchondrotic connection between the endocranium and the palatoquadrate.

The fenestra exonarina anterior (*fe. exa*, figs. 34, 52 B, 57 A, C, D, 58, 68 A, 70 A; pl. 6, figs. 1, 2; pl. 7; pl. 9, figs. 1, 4; pl. 10; pl. 11, figs. 3, 4, 6) is situated between the anterior tectal and lateral rostral outside the antero-ventral part of the considerably larger fenestra endonarina anterior. Generally its posterior corner is low and angular, but sometimes it may be more rounded posteriorly and oval as a whole. Judging from its shape and comparatively small size it can have been traversed by the anterior external nasal tube only. As the close surroundings of the fenestra are ornamented, this tube cannot have extended far along the outside of the ethmoidal shield, and it is thus likely that its external opening, the anterior external nostril, lay immediately outside the fenestra.

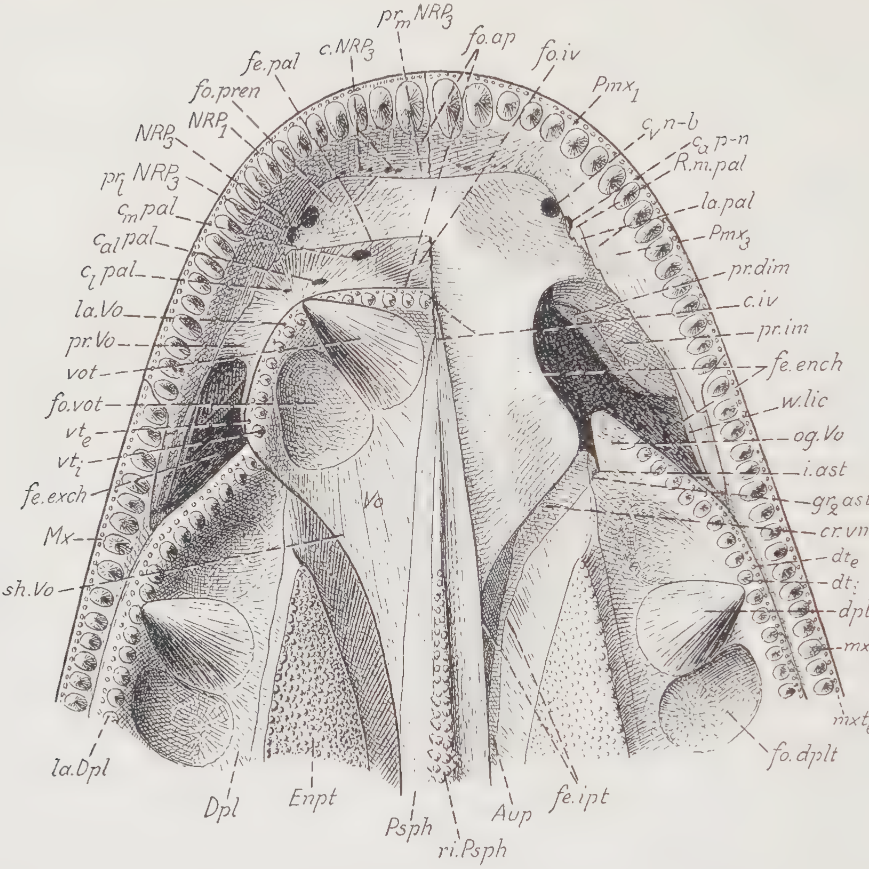
As has been mentioned above, there is no fenestra exonarina posterior on the lateral side of the snout. The posterior external nasal tube (cf. pp. 446—447, 467) most probably opened posteriorly in the soft tissue which stretched from the margin of the orbital opening (*fe. o*, fig. 68 A) to the eye.

The fenestra exochoanalis (*fe. exch*, figs. 56, 57 B, 64 A, 87 A; pl. 8, fig. 1; pl. 12) is a fairly large opening, longer than broad and narrowing posteriorly, situated mainly underneath the postero-lateral part of the fenestra endochoanalis. It is bounded anteriorly by the concave posterior margin (see figs. 52 B, 56) of the broad and thick ridge-like connection between the vomer and the ethmoidal shield (p. 450). The lateral boundary is formed by the hindmost part of the premaxillary, the postero-ventro-lateral corner of the ethmoidal shield overlapped by the lachrymal and the maxillary, and behind that by the foremost part of the maxillary. The medial boundary is formed by the vomer and the dermopalatine. The dermal bones around the fenestra exochoanalis are all high or provided with laminae (*la. Vo*, *la. Dpl*) descending far below the level of the fenestra itself, which in ventral aspect thus lies at the bottom of a deep fossa.

The fossa apicalis (*fo. ap*, figs. 56, 64 A, 87 A; pl. 6, fig. 1; pl. 8, fig. 1; pl. 9, fig. 3; pl. 11, figs. 1, 2) as defined by the writer (Jarvik 1937, pp. 105, 117—118) is a large space open ventrally, situated in the foremost part of the roof of the mouth cavity underneath the divisio prenasalis communis of the ethmoidal region. It is semilunar in ventral view and bounded by dermal bones except for a considerable part of the roof, where the endoskeleton is exposed in a short and broad gap, the anterior palatal fenestra (*fe. pal*). Its anterior wall, which is strongly convex, consists of the descending tooth-bearing parts of the premaxillaries (naso-rostro-premaxillaries). Its posterior wall (see also fig. 58) is fairly straight and composed of a median high part formed by the transverse portions of the descending tooth-bearing laminae of the vomers, and a paired, low lateral part formed by the ridge-like connection between the vomer and the ethmoidal shield (p. 450). The central part of the roof (in the anterior palatal fenestra) is formed by the lower face of the divisio prenasalis communis, its anterior and lateral parts by the lower face of the palatal lamina of the ethmoidal shield, and its posterior parts by the horizontal parts of the vomers stretching forwards in front of the tooth-bearing laminae and the antero-lateral processes (*pr. Vo*). In the fossa apicalis are found the prenasal and intervomerine pits, the former paired, the latter unpaired.

The prenasal pit (*fo.pren*, figs. 48, 56, 58 A, 64 A; pl. 8, fig. 1; pl. 11, fig. 2) lies on the lateral part of the lower face of the divisio prenasalis communis of the ethmoidal region (cf. p. 434). It is bounded anteriorly and laterally by the thickened margin of the palatal lamina of the ethmoidal shield, whereas its hinder part extends backwards onto the lower face of the thin antero-lateral part of the vomer situated in front of the thick antero-lateral process (*pr. Vo*). At the lateral margin of the pit lies the ventral orifice of the ventral branch ($c_v n$-b) of the nasobasal canal (p. 470) and close postero-laterally to that the anterior orifice of the anterior palatonasal canal ($c_a p$-n; p. 473). The part of the vomer forming the roof of the hinder part of the pit is pierced by three foramina which are the anterior orifices of the medial, lateral and antero-lateral branches ($c_m pal$, $c_l pal$, $c_{al} pal$) of the palatine canal (p. 474). It may also be mentioned that the pars palatina of the naso-rostro-premaxillary is pierced by a few fine canals ($c.NRP_3$, fig. 56; pl. 8, fig. 1) immediately in front of the prenasal pit.

The intervomerine pit (*fo. iv*, figs. 56, 58, 64 A, 87 A; pl. 6, fig. 1; pl. 8, fig. 1) is situated on both vomers in the posterior median part of the fossa apicalis. The pit lies in the part of the roof of the fossa apicalis formed by the anterior horizontal parts of the vomers, but also extends onto the posterior wall of the fossa apicalis. It is bounded antero-laterally from the prenasal pit of either side by a thickening of the vomer. The intervomerine pit decreases in width posteriorly and passes over into a short median rostro-caudal canal, the intervomerine canal (*c. iv*, figs. 56, 58 A, 64 A, 87 A; pl. 6, fig. 1; pl. 8, fig. 1), running backwards in the upper part of the suture between the descending tooth-bearing vomerine laminae. The posterior orifice of the canal is situated on the posterior face of the descending tooth-bearing vomerine laminae immediately ventrally to the pointed anterior extremity of the para-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$c_v n$-b
$c_a p$-n
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Fig. 56. *Eusthenopteron foordi* Whiteaves. The anterior parts of the divisio cranialis anterior and the anterior parts of the palatoquadrate-cheek complex in ventral view. Vomer of left side removed. Left medial rostral independent. Restoration based mainly on the specimen shown in pl. 8, fig. 1 and on grinding-series 2. $^7/_2$.

Aup, pars autopalatina of palatoquadrate; *Dpl*, dermopalatine; *Enpt*, entopterygoid; *Mx*, maxillary; NRP_1, NRP_3, pars dentalis and pars palatina of compound naso-rostro-premaxillary; Pmx_1, Pmx_3, pars dentalis and pars palatina of premaxillary proper; *Psph*, parasphenoid; *R. m. pal*, processus palatinus of medial rostral; *Vo*, vomer; $c_a p$-n, anterior palatonasal canal; $c_{al} pal$, antero-lateral branch of palatine canal; *c. iv*, intervomerine canal; $c_l pal$, $c_m pal$, lateral and medial branches of palatine canal; $c.\ NRP_3$, canals piercing pars palatina of naso-rostro-premaxillary; *cr. vm*, ventro medial crista of pars autopalatina; $c_v n$-b, ventral branch of nasobasal canal; *dplt*, dermopalatine tusk; dt_e, dt_i, external and internal rows of dermopalatine teeth; *fe. ench*, fenestra endochoanalis; *fe. exch*, fenestra exochoanalis; *fe. ipt*, interpterygoid fenestra; *fe. pal*, anterior palatal fenestra; *fo. ap*, fossa apicalis; *fo. dplt*, pit of missing dermopalatine tusk; *fo. iv*, intervomerine pit; *fo. pren*, prenasal pit; *fo. vot*, pit of missing vomerine tusk; $gr_2 ast$, groove for postchoanal nerve anastomosis in ventral face of dermopalatine; *i. ast*, notch for postchoanal nerve anastomosis in dermopalatine; *la. Dpl*, lateral tooth-bearing lamina of dermopalatine; *la. pal*, palatal lamina of ethmoidal shield; *la. Vo*, ventral tooth-bearing lamina of vomer; mxt_e, mxt_i, external and internal rows of maxillary teeth; *og. Vo*, area of dermopalatine overlapping vomer; *pr. dim*, processus dermintermedius of lateral rostral; *pr. im*, processus intermedius of lamina nariochoanalis; $pr_l NRP_3$, lateral process sphenoid, which forms the roof of the posterior part of the canal. The medial part of either descending tooth-bearing vomerine lamina near the intervomerine canal is pierced by fine canals, which in the single specimen where they are shown (fig. 58 A; pl. 6, fig. 1) differ in number and development on the right and left sides and must have been traversed by small nerves and vessels.

The foremost part of the cranial cavity (figs. 49, 57 A—C, 59, 70 A) differs in many important features from the corresponding part in *Porolepis* (cf. pp. 362—364). Most posteriorly there issues from it a long pineal canal (*c.pin*) which ascends forwards to a pineal foramen (*f.pin*, figs. 34, 57 A, C) in the dorsal face of the fronto-ethmoidal shield. The division of the cavity situated in front of the basal end of the pineal canal beyond doubt mainly lodged the forebrain and may thus be referred to as the forebrain division (*div.fbr*). This division does not extend forwards into the ethmoidal region but ends anteriorly some distance behind that region. It is comparatively long, hardly wider than the division next behind it and comparatively low. Its breadth slightly exceeds its height which is only about one sixth of the total height of the interorbital wall. The foremost portion of the division, the bulbar portion, (*p.bulb*, figs. 49, 57 A—C, 70 A), has a broad shallow depression in its floor and is thus slightly higher than the posterior portion. It must have been occupied by the bulbi olfactorii, whereas the posterior portion, the hemispheral portion (*p.hem*, fig. 57 A—C), lodged the hemispheres. The hemispheral portion is imperfectly subdivided into right and left halves by low median dorsal and ventral longitudinal ridges. The dorsal ridge does not extend forwards onto the bulbar portion, but terminates at the transition to that portion. The ventral ridge, on the other hand, is traceable forwards also throughout the bulbar portion, which therefore is incompletely divided into right and left halves on its ventral side only. The ridge is very slightly developed in the posterior part of the bulbar portion, but increases considerably in height forwards (ri_v, figs. 49, 70 A) and finally passes over into the posterior continuation (*s.olf*; p. 439) of the internasal wall which separates the olfactory canals.

The canalis olfactorius (*c.olf*, figs. 49—51, 57, 59, 65 A, 70 A; pl. 12, figs. 4—6; pl. 13, figs. 1—5) goes forwards and somewhat laterally to

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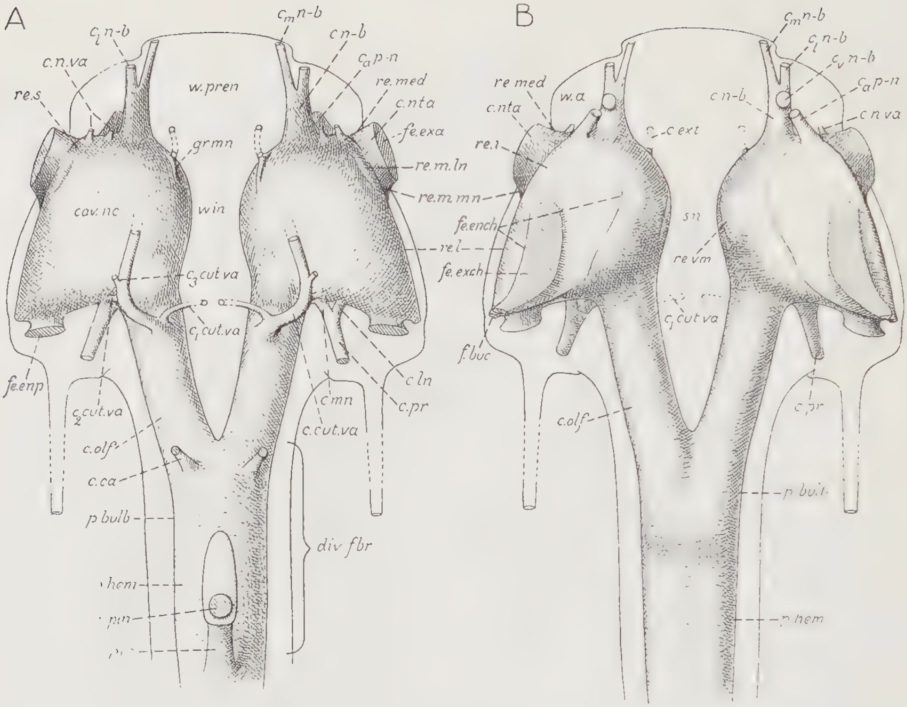
of pars palatina of naso-rostro-premaxillary or lateral paired process of palatal lamina of ethmoidal shield; pr_mNRP_3, medial process of pars palatina of naso-rostro-premaxillary or lateral half of median unpaired process of palatal lamina of ethmoidal shield; *pr. Vo*, antero-lateral process of vomer; *ri. Psph*, tooth-bearing ridge of parasphenoid; *sh. Vo*, vomerine shelf; *vot*, vomerine tusk; vt_e, vt_i, external and internal rows of vomerine teeth; *w. lic*, ventral medially curved part of lateral nasal wall.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$c_a p$-n
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grmn
re.m.ln
re.m.mn
cav.nc
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fe.enp
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c.olf
c.ca
p bulb
hem
pin
c ln
c.pr
c mn
c.cut.va
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$c_a p$-n
c n va
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c ext
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re.m.mn
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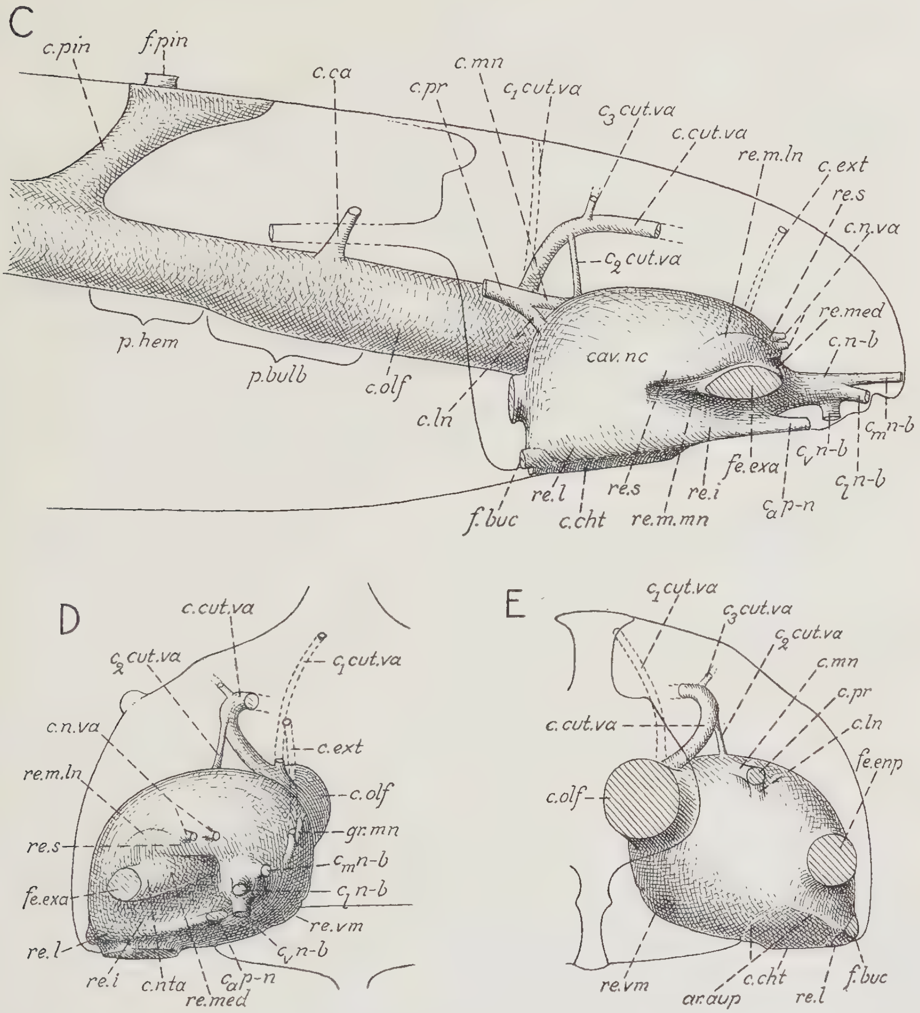
sn
re vm
$c_1$cut va
f.buc
c.olf
c.pr
p bulb
p hem

Fig. 57. *Eusthenopteron foordi* Whiteaves. *A—C*, cast of the anterior part of the cranial cavity and of the olfactory canals and nasal cavities in their position in relation to the endocranium. *A*, dorsal, *B*, ventral, *C*, lateral view. *D*, *E*, cast of the right nasal cavity. *D*, anterior, *E*, posterior view. Endocranium shown in outline. Restorations mainly after grinding-series 1 and 2. *A* and B, $^5/_2$. *C—E*, $^{10}/_3$.

ar. aup, extent of the area of nasal cavity below the postnasal wall that is bounded by the pars autopalatina of the palatoquadrate; $c_a p$-n, anterior palatonasal canal; *cav. nc*, nasal cavity; *c. ca*, canal for v. cerebralis anterior; *c. cht*, canal for choanal tube; *c. cut. va*, canal for cutaneous vessel; c_1*cut. va*, c_2*cut. va*, c_3*cut. va*, first, second, and third branch of ditto; *c. ext*, canal for r. externus narium of n. profundus; *c. ln*, *c. mn*, canals for r. lateralis and r. medialis narium of n. profundus; $c_l n$-b, $c_m n$-b, lateral and medial branches of nasobasal canal; *c. n-b*, nasobasal canal; *c. nta*, canal for anterior nasal tube; *c. n. va*, canals for nerves or vessels; *c. olf*, canalis olfactorius; *c. pin*, pineal canal; *c. pr*, profundus canal; $c_v n$-b, ventral branch of nasobasal canal; *div. fbr*, forebrain division of cranial cavity; *f. buc*, opening for r. buccalis lateralis; *fe. ench*, fenestra endochoanalis; *fe. enp*, opening probably representing fenestra endonarina posterior; *fe. exa*, fenestra exonarina anterior; *fe. exch*, fenestra exochoanalis; *f. pin*, pineal foramen; *gr. mn*,

its funnel-shaped orifice into the postero-medial corner of the nasal cavity. It is about as high as the bulbar portion of the cranial cavity, slightly higher than broad and a little oval or almost circular in transverse sections.

The development of the forebrain division and the olfactory canals (fig. 57 A—C) prompt the following conclusions as to the general characters of the forebrain and the olfactory nerve (fig. 59). The hemi-


C
c.pin
f.pin
c.ca
c.mn
c.pr
c_1 cut.va
c_3 cut.va
c.cut.va
re.m.ln
c.ext
re.s
c.n.va
c_2 cut.va
re.med
c.n-b
cav.nc
p.hem
p.bulb
c.olf
c.ln
c_mn-b
c_vn-b
fe.exa
c_ln-b
c_ap-n
re.l
re.s
re.i
f.buc
c.cht
re.m.mn
D
c.cut.va
c_2 cut.va
c_1 cut.va
c.n.va
re.m.ln
c.ext
c.olf
gr.mn
c_mn-b
c_ln-b
re.s
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fe.enp
c.cut.va
c.olf
re.vm
c.cht
ar.aup
re.l
f.buc

groove for r. medialis narium; *p. bulb*, bulbar portion of cranial cavity; *p. hem*, hemispheral portion of cranial cavity; *re. i*, recessus inferior of nasal cavity; *re. l*, recessus lateralis of nasal cavity; *re. med*, recessus medius of nasal cavity; *re. m. ln*, *re, m. mn*, recesses for m. lateralis and m. medialis narium; *re. s*, recessus superior of nasal cavity; *re. vm*, ventro-medial recess of nasal cavity; *sn*, septum nasi; *w. a*, prenasal wall; *w. in*, internasal wall; *w. pren*, divisio prenasalis communis.

spheres (*hem*) must have been of a long, slender and low type, and were separated from each other both dorsally and ventrally by a median groove or slit, a fissura sagittalis (*fiss*). The bulbi olfactorii (*b. olf*) were short and narrow but comparatively high. They must have lain immediately in front of the hemispheres and were probably fused with one another dorsally but separated ventrally by a median sagittal groove which was shallow posteriorly but rapidly increased in depth anteriorly. The olfactory nerve (I) was long and strongly developed and on entering the nasal cavity broke up into several branches to the nasal sac.

The nasal cavity (*cav. nc*, figs. 47, 48, 51—53, 56, 57, 59, 70 A, 71 A, 72 A; pl. 8, fig. 1; pl. 9, fig. 3; pl. 11, figs. 3—6; pl. 12, figs. 1—6) lies in the middle lateral part of the ethmoidal region and is not very far from the corresponding cavity of the other side from which it is separated by a solid septum nasi (p. 439). The cavity consists of a main chamber and several recesses. In its anterior and antero-lateral parts may be distinguished a recessus superior, a recessus inferior, and between the antero-lateral parts of these two recesses, a recessus medius. In addition there are also a recessus ventro-medialis, a recessus lateralis, and two small recesses, conceivably for m. medialis and m. lateralis narium.

The shape of the main chamber is clearly shown in several of the figures (figs. 51—53, 57, 59, 70 A, 71 A) and a detailed description of it is superfluous. It is longer than broad and high, longer laterally than medially, broader posteriorly than anteriorly. The longitudinal axis of the chamber rises slightly forwards and approaches the median plane of the endocranium. The transverse axis of the chamber is not horizontal, but slopes in a lateral direction (fig. 57 D, E). In consequence the postero-ventro-lateral corner of the chamber, which is somewhat extended in a posterior direction, is the most ventrally situated part.

The recessus superior (*re. s*, figs. 52 B, 53, 57 A, C, D, 71 A, 72 A; pl. 11, figs. 3, 6; pl. 12, figs. 1, 2) consists of the anterior dorsal and anterior dorso-lateral parts of the nasal cavity, which are situated dorsally to the crista intermedia (*cr. im*), the lamina superior (*la. s*), and the processus dermintermedius (*pr. dim*), with the exception of the small spaces (*re. med*, *re. m. mn*) just ventrally to the recurved portion (*pr. dim*$_{rc}$) and to the medial process (*pr. Te*) of the anterior tectal. The recessus superior as thus defined is bounded anteriorly by the dorsal division (*w. a*$_1$, fig. 52 C) of the posterior face of the prenasal wall, dorsally by an antero-lateral part of the lower face of the tectum nasi, and laterally by an antero-dorsal part of the medial face of the lateral nasal wall. The recess may be considered to be composed of two parts, one medial and one lateral. The medial part lies above the crista intermedia and reaches medially to the septum nasi. It is very short, its rostro-caudal extent being only slightly larger than that of the crista intermedia. The lateral part extends from above the lamina superior (*la. s*) backwards to above the hindmost end of the posterior horizontal portion of the processus dermintermedius and the posterior end of the medial process (*pr. Te*) of the anterior tectal. This part is broad anteriorly, but narrows backwards as the processus dermintermedius decreases in breadth in that direction. It is lowest anteriorly above the lamina superior, attains its maximum height above the middle main portion of the processus dermintermedius, and then decreases somewhat in height in a posterior direction. From the highest portion a short canal for the anterior external nasal tube (*c. nta*, fig. 57 A, B, D) leads outwards through the fenestra exonarina anterior (*fe. exa*). Dorsally to the medial end of this canal and in the area of the medial face of the anterior tectal closing the upper part of the fenestra endonarina anterior lies the shallow recess (*re. m. ln*) described above (p. 449), which presumably was the place of origin of the m. lateralis narium. Between the medial process (*pr. Te*) of the anterior tectal and the posterior horizontal portion of the processus dermintermedius there is another small recess (*re. m. mn*; p. 449), which opens medially into the main chamber and anteriorly into the recessus superior and probably was the place of origin of the m. medialis narium.

The recessus medius (*re. med*, figs. 52 B, 57 A—D, 58 B, 71 A, 72 A; pl. 11, figs. 3, 6) comprises only the small space open posteriorly and postero-laterally that lies immediately below the recurved portion (*pr.* dim_{rc}) of the processus dermintermedius and between the anterior lateral parts of the recessus superior and inferior. It is bounded also ventrally and anteriorly by the processus dermintermedius and extends from laterally and antero-ventrally in a direction medially and postero-dorsally. Obviously, it constitutes only a small anterior extension of the high middle portion of the lateral part of the recessus superior and lies medially to the foremost part of the fenestra exonarina anterior.

The recessus inferior (*re. i*, figs. 52 B, 53, 57 B—D, 71 A, 72 A; pl. 11, figs. 4, 6) includes the anterior and antero-lateral parts of the nasal cavity which lie ventrally to the crista intermedia (*cr. im*), processus intermedius (*pr. im*, *pr.* im_h), and processus dermintermedius (*pr. dim*), and thus has an extent forwards, backwards and towards the sides corresponding to that of the recessus superior. Like that it consists of a medial and a lateral part. The medial part, which is situated ventrally to the corresponding part of the recessus superior, is bounded dorsally by the crista intermedia, medially by the lateral face of the septum nasi, anteriorly by the ventro-medial division (*w.* a_3, fig. 52 C) of the posterior face of the prenasal wall, laterally by the foremost part of the processus intermedius and ventrally by the antero-medial part of the solum nasi. The lateral part of the recess is bounded dorso-laterally by the most dorso-medially extending part of the processus dermintermedius and by the processus intermedius (see figs. 53, 56) and thus extends backwards as far as those processes. Owing to the oblique position of the processus intermedius it decreases in height laterally, where it is very low. Its anterior end, which is situated laterally to the transition between the medial part of the recess and the main chamber of the nasal cavity, is bounded by the processus intermedius, which at its transition into the prenasal wall forms a face directed somewhat posteriorly. The lateral part of the recessus inferior is devoid of an endoskeletal floor but is closed antero-ventrally by the ridge-like connection between the palatal lamina of the ethmoidal shield and the vomer (see p. 450 and fig. 56). Behind this connection it opens downwards into the mouth cavity through the anterior part of the fenestra exochoanalis (*fe. exch*). From the recessus inferior two canals lead forwards, the nasobasal canal (*c. n-b*) from the medial part, and the anterior palatonasal canal ($c_a p$-n) from the lateral part.

The recessus ventro-medialis (*re. vm*, figs. 52 A, 57 B, D, E, 70 A, 71 A; pl. 11, figs. 4, 5; pl. 12, fig. 1; cf. p. 439) is a wide shallow depression in the ventral part of the medial side of the main chamber of the nasal cavity, that is in the middle ventral part of the septum nasi and an adjacent part of the solum nasi.

The recessus lateralis (*re. l*, figs. 51, 57 A—E) occupies the posterior ventro-lateral part of the nasal cavity behind the lateral part of the recessus inferior. It lies laterally to the part of the main chamber from which the short, wide canal for the choanal tube (*c. cht*, fig. 57 C) leads down to the mouth cavity through the fenestra exochoanalis, and is bounded both laterally and ventrally by the medially curved ventral part (*w. lic*) of the lateral nasal wall. It passes over forwards into the lateral part of the recessus inferior, whereas backwards it is in communication with the mouth cavity through the postero-lateral part of the fenestra endochoanalis and the underlying narrow part of the fenestra exochoanalis.

From the development of the nasal cavity we may infer the following concerning the shape of the nasal sac (*sac n*, figs. 59, 72 A). The main chamber and the high posterior portion of the lateral part of the recessus superior of the nasal cavity were at least to a very large extent occupied by a division of the nasal sac which may be termed the diverticulum principale. From the posterior ventral part of the diverticulum principale the choanal tube issued through the endochoanal and exochoanal fenestrae (the canal *c. cht*) and opened in the roof of the mouth through the internal nostril or choana. The part of the diverticulum principale situated in the recessus superior, the vestibular portion (*vest*), gave off the anterior external nasal tube (*nta*), which went in a lateral direction through the anterior endonarial and exonarial fenestrae (the canal *c. nta*) and opened outwards through the anterior external nostril (*na*). The posterior external nasal tube (*ntp*, fig. 59; *dnl*, fig. 72 A) left the vestibular portion of the diverticulum principale fairly close behind the medial orifice of the anterior external nasal tube. It went backwards dorsally to the posterior horizontal portion of the processus dermintermedius and presumably left the nasal cavity through the fenestra endonarina posterior (*fe. enp*, figs. 49, 50) in the ventro-lateral part of the postnasal wall. From this fenestra it then reached the anterior ventro-lateral part of the orbit where it turned somewhat laterally[1] and continued to the foremost part of the orbital opening. Its posterior orifice, the posterior external nostril, must have been in the soft tissue between the posterior margin of the ethmoidal shield and the eye-ball just in front of the eye, and consequently the posterior external nasal tube must in all probability have been modified into a true nasolachrymal duct. The diverticulum principale was certainly continuous anteriorly and antero-laterally with sac-like bulges which occupied the recessus inferior and the anterior parts of the recessus superior and which may be termed the diverticulum inferius (*di. i*) and the saccus superior (*di. s*). Immediately in front of the internal orifice of the anterior external nasal tube the vestibular portion of the diverticulum principale was probably provided with a small anterior bulge, the diverticulum medium (*di. med*, figs. 59, 72 A), which filled the recessus medius. The diverticulum medium was thus situated between the anterior lateral parts of the saccus superior and diverticulum inferius and its lateral part lay somewhat further forwards than its medial one. The medial lower part of the diverticulum principale was slightly bulged, forming a diverticulum mediale in the ventro-medial recess of the nasal cavity, close behind the anterior medial part of the diverticulum inferius. Finally, the diverticulum principale was also equipped with a postero-ventro-lateral bulge, the diverticulum laterale (*di. l*, fig. 59), which lay ventrally to the posterior external nasal tube, behind the diverticulum inferius, and immediately dorso-laterally to the fenestra endochoanalis, and occupied the whole lateral recess of the nasal cavity. The diverticulum laterale formed a direct posterior continuation of the postero-lateral part of the diverticulum inferius and enclosed a groove-like part of the cavity of the nasal sac, the sinus lateralis nasi, which probably opened medioventrally into the choana and posteriorly into the cavity of the mouth. It was possibly continued backwards by a short sulcus maxillo-palatinus bounded ventrally by a small plica palatina (cf. p. 536).

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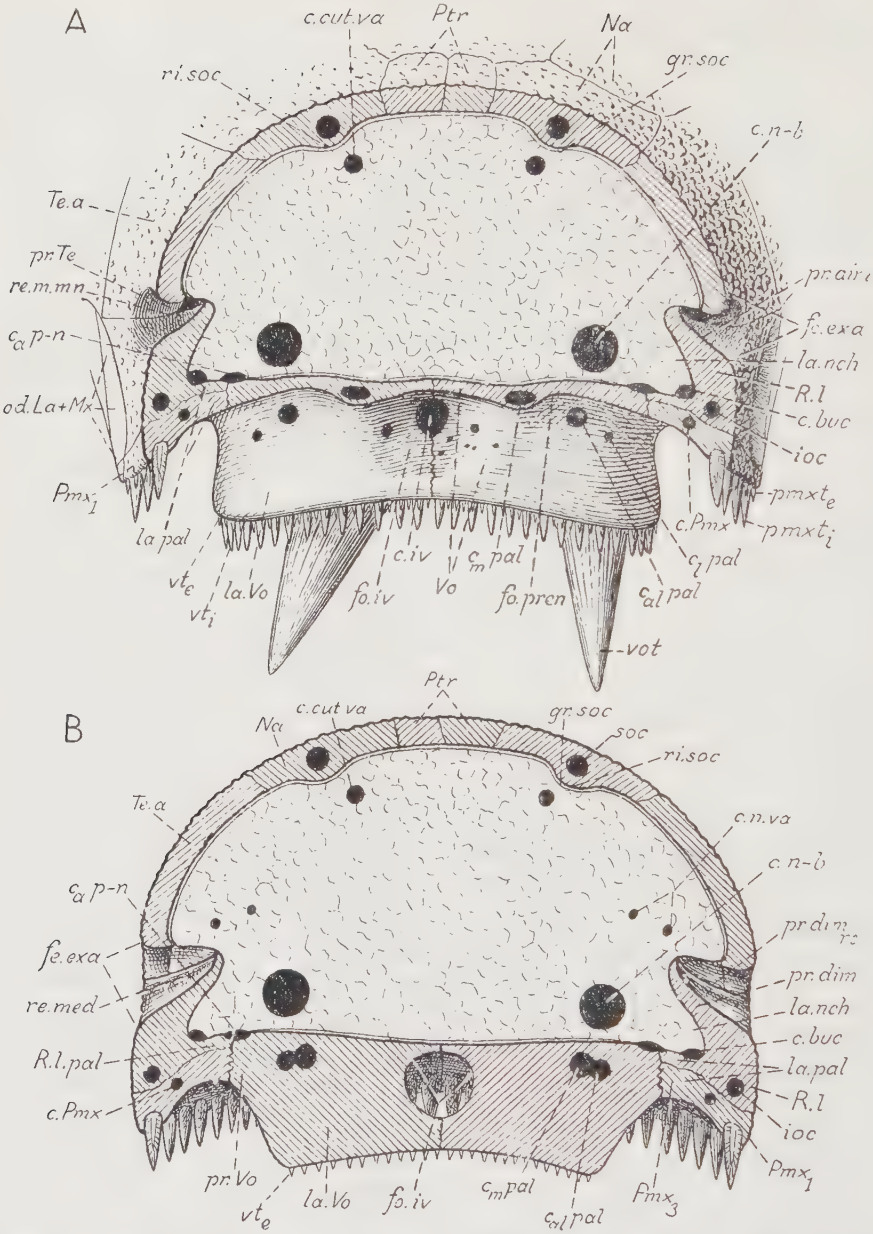
[1] The posterior part of the tube is incorrectly restored in this respect in fig. 59.


A
c.cut.va
Ptr
Na
gr.soc
ri.soc
c.n-b
Te.a
pr.Te
re.m.mn
c_a p-n
od.La+Mx
Pmx_1
la.pal
vt_e
vt_i
la.Vo
fo.iv
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c_{al} pal
c_l pal
c.Pmx
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Pmx_1
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fo.iv
c_m pal
c_{al} pal
Pmx_3

Fig. 58. *Eusthenopteron foordi* Whiteaves. *A*, snout seen from front, the tip removed by a transverse section immediately in front of the anterior transverse part of the vertical tooth-bearing lamina of the vomer. *B*, snout seen from behind with the posterior parts removed by a transverse section through the anterior transverse part of the vertical tooth-bearing lamina of the vomer. Restorations after the grinding-series and several specimens. $\frac{4}{1}$.

Na, nasal; *Pmx*$_1$, *Pmx*$_3$, pars dentalis and pars palatina of premaxillary; *Ptr*, postrostral; *R. l*, lateral rostral; *R. l. pal*, processus palatinus of lateral rostral; *Te. a*, anterior

It now remains to describe the various canals and other passages for nerves and vessels in the snout.

Apart from the canalis olfactorius already described (p. 461) only one canal worth mentioning is found in the anterior part of the interorbital wall. This canal (*c. ca*, figs. 47 A, B, 49, 55, 57 A, C; pl. 8, fig. 2; pl. 10; pl. 13, fig. 5), which must be assumed to have transmitted the v. cerebralis anterior, runs on either side from the bulbar portion of the cranial cavity upwards, forwards and laterally through the cranial wall to the anterior dorsal part of the orbit.

A little behind the postero-medial corner of the nasal cavity the canalis olfactorius gives off a comparatively wide canal on its dorsal side. This canal, *c. cut. va* (figs. 51, 52 A, C, 53, 57, 58, 71 A; pl. 11, figs. 3—5; pl. 12, figs. 3—6; pl. 13, fig. 1), ascends in a somewhat oblique antero-dorsal direction towards the groove *gr. soc* on the dorsal face of the ethmoidal region. Before reaching this groove, however, it curves strongly forwards and continues in an anterior and slightly medial direction in the tectum nasi somewhat ventro-medially to the groove.

In grinding-series 1 it could be traced as far forwards as about opposite the anterior part of the fenestra endonarina anterior. The canal sends out several branches. The first ($c_1 cut. va$, figs. 47 A, C, 57; pl. 12, fig. 5), which is given off close above the olfactorius canal, goes upwards and somewhat medially towards the dorsal face of the ethmoidal region where it probably had its external orifice close to the orifice of the corresponding branch of the opposite side (fig. 47 A, C). The second branch ($c_2 cut. va$, figs. 51, 57 A, C—E), observed in grinding-series 1 only, issues from the bend between the ascending part of the canal and the part directed forward, and goes down to the posterior dorsal part of the nasal cavity. A third branch ($c_3 cut. va$, figs. 47, 57 A, C, E), which issues a little in front of the second one, ascends to the groove *gr. soc*, thence continuing into the above-lying dermal bone (probably the nasal 7; cf. fig.

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tectal; *Vo,* vomer; $c_{al}pal$, antero-lateral branch of palatine canal; $c_a p$-n, anterior palatonasal canal; *c. buc,* canal for r. buccalis lateralis; *c. cut. va,* canal for cutaneous vessel; *c. iv,* intervomerine canal; $c_l pal$, $c_m pal$, lateral and medial branches of palatine canal; *c. n-b,* nasobasal canal; *c. n. va,* canals for nerves or vessels; *c. Pmx,* canal for nerve to premaxillary teeth; *fe. exa,* fenestra exonarina anterior; *fo. iv,* intervomerine pit; *fo. pren,* prenasal pit; *gr. soc,* groove for supraorbital sensory canal ridge; *ioc,* infraorbital sensory canal; *la. nch,* lamina nariochoanalis; *la. pal,* lamina palatina of ethmoidal shield; *la. Vo,* vertical tooth-bearing lamina of vomer; *od. La+Mx,* area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; $pmxt_e$, $pmxt_i$, external and internal rows of premaxillary teeth; *pr. dim,* processus dermintermedius of lateral rostral; $pr. dim_{rc}$, anterior recurved portion of processus dermintermedius; *pr. Te,* medial process of the anterior tectal extending into nasal cavity; *pr. Vo,* antero-lateral process of vomer; *re. med,* recessus medius of nasal cavity; *re. m. mn,* recess for m. medialis narium; *ri. soc,* supraorbital sensory canal ridge; *soc,* supraorbital sensory canal; *vot,* vomerine tusk; vt_e, vt_i, external and internal rows of vomerine teeth.

34). During its further passage forwards the canal *c. cut. ra* gives off still more branches (pl. 12, fig. 3), but these are still very imperfectly known. It would appear that the canal was developed for a vessel, probably a vein, receiving tributaries from the dermal bones and the skin on the upper side of the snout and from the nasal cavity.

Laterally to the most dorsal part of the canalis olfactorius the postnasal wall is pierced by a canal which, judging from its position, must be the profundus canal (*c. pr*, figs. 48—51, 57 A, B, C, E, 59, 65 A; pl. 8, figs. 1, 2; pl. 9, fig. 3; pl. 10; pl. 12, figs. 5, 6; pl. 13, figs. 1—3). This canal goes in an anterior and somewhat medial direction through the postnasal wall from the orbit to the postero-dorsal part of the nasal cavity. In certain cases it breaks up into two branches (grinding-series 2, right side), one dorso-medial and one ventro-lateral, which are the canals for the r. medialis narium (*c. mn*) and the r. lateralis narium (*c. ln* figs. 51, 57 A—C; pl. 12, fig. 4). The groove *gr. mn* (p. 439; figs. 47 B, 52 A, C, 57 A, D) in the anterior part of the medial face of the nasal cavity has such a position that it must be assumed to have lodged the r. medialis narium. The canal for the r. externus narium (*c. ext*, figs. 47 B, 52 A, C, 57 B—D, 67 A, 71 A; pl. 11, fig, 3) issues from the groove *gr. mn* in a direction upwards and forwards. It could be followed only a short distance (gr.-ser. 1), but probably pierced the ethmoidal region and opened on its dorsal face close medially to the groove *gr. soc.*

The groove *gr. mn* terminates slightly postero-dorso-medially to the posterior orifice of the canalis nasobasalis (*c. n-b*, figs. 52, 57 A—C, 58, 59, 71 A; pl. 9, figs. 3, 4; pl. 11, figs. 2—4) and it is obvious that the r. medialis narium must have left the nasal cavity through the canalis nasobasalis. Piercing the ventral medial part of the prenasal wall this canal leads from the medial part of the recessus inferior of the nasal cavity forwards and slightly medially to the tip of the snout. Its anterior part breaks up into a medial ($c_m n\text{-}b$) and a lateral ($c_l n\text{-}b$) branch (figs. 47 C, 57 A—D, 59; pl. 11, fig. 2). The medial branch opens anteriorly on the lateral corner of the dorsal rostral process (*pr. rd*), the lateral branch in the posterior wall of the groove $gr_c ioc$ close to the lateral corner of the ventral rostral process (*pr. rv*). Just before breaking up into its medial and lateral branches the nasobasal canal gives off a short comparatively wide ventral branch ($c_v n\text{-}b$, figs. 48, 56, 57 B—D, 64 A; pl. 8, fig. 1; pl. 9, fig. 3; pl. 11, figs. 2, 3) which goes down to the ventral face of the ethmoidal region where it opens in the prenasal pit (*fo. pren*) in the lateral part of the roof of the fossa apicalis (*fo. ap*).

From the recessus superior of the nasal cavity two fine canals (*c. n. va*, figs. 52 A, C, 57 A—D, 58 B) pass forward into the lateral half of the prenasal wall. They could be traced only a short distance forwards in one of the grinding-series (gr.-ser. 1) and must have transmitted nerves or vessels or both.

The canal for the r. ophthalmicus lateralis (*c. o. lat*, figs. 47, 49, 50; pl. 7, fig. 2; pl. 8, fig. 2; pl. 13, figs. 1, 2) has its posterior orifice on the posterior face of the postnasal wall above the profundus canal, close below the lamina supraorbitalis (p. 436). It passes forwards in the postnasal wall close ventrally to the hindmost part of the groove *gr. soc*, but owing to the imperfect ossification of the superficial postero-dorso-lateral part of the ethmoidal region (*cart*) it could be followed only a short distance forwards in the grinding-series (gr.-ser. 1 and 2). As it is not found further forwards where the ethmoidal region is completely ossified in its superficial parts, the canal must obviously have reached the dorsal face of the ethmoidal region pretty soon and was thus in all probability short. In front of the canal the r. ophthalmicus lateralis must have passed forwards between the ethmoidal shield and the ethmoidal region. Judging from the position of the fine canals for its branches to the sensory canal organs in the nasal elements it lay in the medial part of the groove *gr. soc*. Somewhat behind its probable anterior orifice (the foramen *c. o. lat*, fig. 47) the canal gives off a short but fairly wide dorsal branch (c_7*o. lat*, fig. 47; pl. 7, fig. 2; pl. 8, fig. 2; pl. 13, fig. 1) which ascends to the hindmost part of the groove *gr. soc*. This branch is continued to the supraorbital sensory canal by a canal in the above-lying nasal 7 (cf. fig. 34).

From the dorso-lateral part of the posterior face of the postnasal wall two fine canals for profundus branches ascend to the hindmost part of the dorsal face of the ethmoidal region. These two canals, which are the canal for the r. frontalis perforans (*c. perf*, figs. 47, 49, 50; pl. 7, fig. 2; pl. 8, fig. 2) and the canal for the r. frontalis anterior (*c. fra*), have thus far been observed in a single specimen (P. 341) only (cf. p. 436). The former (*c. perf*) lies dorso-medially, the latter (*c. fra*) ventro-laterally to the canal for the r. ophthalmicus lateralis (*c. o. lat*).

In addition to the canals described, all of which pierce the endocranium, the snout presents several other canals for nerves and vessels outside the endocranium itself. Many of the latter canals have such relations to each other and to various grooves, slits and openings that long passages, more or less clearly continuous, are formed for nerves and vessels. Among these passages we shall first turn to the one which was developed for the r. buccalis lateralis.

In the middle parts of the lachrymal the bony medial wall of the infraorbital sensory canal (*ioc*, fig. 55; pl. 13, fig. 5) is pierced by a fine canal coming from the lowermost antero-lateral part of the orbit. This canal ($c_{La_2}buc$) was beyond doubt traversed by a branch from the r. buccalis lateralis to one of the sensory organs of the infraorbital canal. It is thus evident that the r. buccalis lateralis must have passed forwards in the anterior ventro-lateral part of the orbit close to the dorso-lateral margin of the pars autopalatina. At the very antero-ventro-lateral corner of the orbit and almost straight in front of the medial opening of the fine nerve canal ($c_{La_2}buc$) just described there is a comparatively small opening, *f. buc* (fig. 55; pl. 13, fig. 1; see also fig. 65 A), which is bounded dorso-medially by the postero-ventral process (*pr. pv*) of the ethmoidal region, ventro-medially by the antero-dorsal process (*pr. Mx*) of the maxillary, and laterally by the posterior tectal (or tectal component of the supraorbito-tectal). Close antero-medially to that opening lies the notch *i. buc* (figs. 47 B, 48) in the postero-ventral corner of the lateral nasal wall. From the small space between the opening *f. buc* behind and the notch *i. buc* in front there issues a fine canal for a branch of the r. buccalis lateralis to a sensory organ in the infraorbital sensory canal in the preorbital part of the lachrymal (cf. *ioc*, pl. 12, fig. 4). The presence of this fine canal shows that the r. buccalis continued in front of the orbit through the opening *f. buc.* In front of that it ran forwards and entered the lateral recess of the nasal cavity through the notch *i. buc.* From the lateral recess it continued forwards to the very rostral part of the snout in a groove (*gr. buc*, figs. 47 B, 48, 52 C; cf. p. 434) extending forwards on the lower side of the lamina nariochoanalis and the ventro-lateral side of the crista subnasalis. This groove is covered by the palatal lamina of the ethmoidal shield, whereby a distinct canal (*c. buc*, figs. 53, 58, 71 A; pl. 11, figs. 1, 2) is formed between the endoskeleton and the exoskeleton. Fine branches issue from this canal to the parts of the infraorbital sensory canal enclosed in the lateral and medial rostrals and evidently transmitted buccalis branches to the sensory canal organs. One of these fine canal branches is shown in the section, fig. 53 ($c_{R.l}buc$).

In the dorso-lateral crest of the dermopalatine there is a rostro-caudal canal, *c. ast* (figs. 54 B, 55, 65 A; pl. 10; pl. 13, figs. 2—5), termed the canal for the postchoanal anastomosis (p. 453). I have not been able to ascertain, where this canal has its posterior (orbital) orifice in the dermopalatine. It can be traced, however, through the anterior part of the dermopalatine (gr.-ser. 2) to its anterior orifice in the medial side of the dorso-lateral crest of the dermopalatine close in front of the place where this crest begins to diverge from the pars autopalatina of the palatoquadrate (fig. 54 B). This canal is continued forwards by the groove gr_1ast, which passes in an oblique medial and ventral direction to the small notch *i. ast* (figs. 54 B, 56) in the medial margin of the dermopalatine, from which the short groove gr_2ast (fig. 56) leads backwards and somewhat medially on the lower side of the dermopalatine. The groove gr_2ast runs towards the place where the r. palatinus VII entered the palatine canal (see p. 480). The canal *c. ast* and the grooves gr_1ast and gr_2ast, including the notch *i. ast*, thus form a continuous passage from the orbit forwards, medially and downwards to the roof of the mouth cavity. The passage goes along the lateral margin of the pars autopalatina laterally and antero-laterally to the connection between the lateral autopalatine articular area (art_1l) of the postnasal wall and the lateral ethmoidal articular area (art_2l) of the pars autopalatina, along the anterior part of the thick postero-lateral part of the ventral margin of the postnasal wall, and behind the anterior tip of the dermopalatine. Judging from its position this passage was developed for an anastomosis between the r. maxillaris V and the r. palatinus VII behind the choana. This anastomosis will be referred to as the postchoanal anastomosis (see p. 477).

Immediately antero-ventro-medially to the notch *i. ast* in the dermopalatine a canal (*c. vot*, pl. 8, fig. 2; pl. 9, fig. 2) begins in the vomer and runs forward to the pulp-cavity of one of the vomerine tusks. This canal seems to have transmitted a branch from the postchoanal anastomosis to the said vomerine tusk.

The posterior palatonasal canal ($c_pp\text{-}n$, figs. 54, 65 A) has been described above (p. 454). Its anterior orifice has a somewhat varying position, but as a rule it seems to be situated at the dorsal margin of the dorso-lateral crest of the dermopalatine somewhat behind the anterior opening of the canal for the postchoanal anastomosis (*c. ast*), and, when the palatoquadrate-cheek complex is in its natural position, close behind the opening *f. buc* (see p. 472) in the anterior ventro-lateral corner of the orbit. The nerve which traversed the posterior palatonasal canal may therefore be assumed to have entered the opening *f. buc* together with the r. buccalis lateralis. In its further course forwards this nerve may have accompanied the r. buccalis lateralis into the lateral recess of the nasal cavity. It is much more likely, however, that it continued forwards ventrally to the nasal capsule in the ventrally open groove-like slit between the ventral medially curved part (*w. lic*) of the lateral nasal wall and the lowermost part of the lateral rostral (cf. figs. 52 B, 56). At any event this groove-like slit leads forwards towards the anterior palatonasal canal ($c_ap\text{-}n$, figs. 52 B, 56, 57 A—D, 58, 71 A; pl. 8, fig. 1; pl. 9, figs. 3, 4; pl. 11, figs. 3, 4). This canal goes from the lateral part of the recessus inferior forwards to the prenasal pit, passing between the ethmoidal region and the underlying dermal bones. More precisely it is bounded above by the groove *gr. p-n* (fig. 48; p. 434) in the ethmoidal region and below by the antero-lateral process (*pr. Vo*; see p. 451) of the vomer and the lateral process of the palatal lamina of the ethmoidal shield ($pr_l NRP_3$). It passes just above the suture between these two processes and has about the same extent forwards and backwards as the posterior unbranching part of the nasobasal canal (*c. n-b*) dorso-medially to it. The posterior palatonasal canal, the ventrally open slit-like groove between the ventral parts of the lateral nasal wall and the lateral rostral, and the anterior palatonasal canal thus form an almost continuous passage laterally to the fenestra exochoanalis from the orbit to the prenasal pit, conceivably for a branch of the r. maxillaris V (r. palatonasalis; see p. 477).

The premaxillary and at least the larger anterior part of the maxillary are pierced in a longitudinal direction by a more or less distinct canal (*c. Pmx*, *c. Mx*, figs. 52 B, 53, 55, 58, 65 A, 68 A, E; pl. 6, fig. 2; pl. 7, fig. 1; pl. 8, fig. 3; pl. 9, fig. 4; pl. 10; pl. 11, figs. 3, 6; pl. 12, figs. 1, 5, 6; pl. 13, fig. 5) from which branches descend to the pulp-cavities of the teeth of the premaxillary and maxillary. The canal leaves the premaxillary posteriorly on the lower part of the overlapped area (*od. La + Mx*) at the postero-ventro-lateral corner of the ethmoidal shield (cf. p. 448), whence it continues backwards in the maxillary. It is difficult to trace in the grinding-series and it could not be established whether it has any definite posterior opening on the medial face of the maxillary. Since its medial wall is pierced by several narrow canals (see fig. 55; pl. 13, fig. 5) it is likely, however, that the canal lodged nerves and vessels which entered it at different places and not all at once through a common large opening.

The palatine canal (*c. pal*, fig. 53; pl. 9, fig. 2; pl. 11, figs. 3, 4, 6) begins posteriorly at the postero-lateral margin of the vomer somewhat postero-medially to the posterior end of the descending tooth-bearing lamina of that bone and goes forwards first between the vomer and the ethmoidal region and then, in its anterior part, within the vomer. The posterior part between the vomer and the ethmoidal region is bounded below by a groove (*gr. pal*, pl. 9, fig. 2; pl. 11, fig. 5) in the dorsal face of the vomer and stretches forwards only to about opposite the middle of the rostro-caudal part of the tooth-bearing lamina (*la. Vo*) of the vomer, where it passes over into the anterior part of the canal completely enclosed in the vomer. Here the canal fairly soon divides into a medial ($c_m pal$) and an antero-lateral branch ($c_{al} pal$), the latter with a still more lateral branch ($c_l pal$, figs. 56, 58, 64 A; pl. 6, fig. 1; pl. 8, figs. 1, 3; pl. 9, figs. 2—4). The anterior orifices of these three branches are situated in the prenasal pit in the roof of the fossa apicalis (cf. p. 459).

Immediately behind the posterior orifice of the palatine canal there is an ascending canal (*c. a. obl*, fig, 55) which leads upwards from the

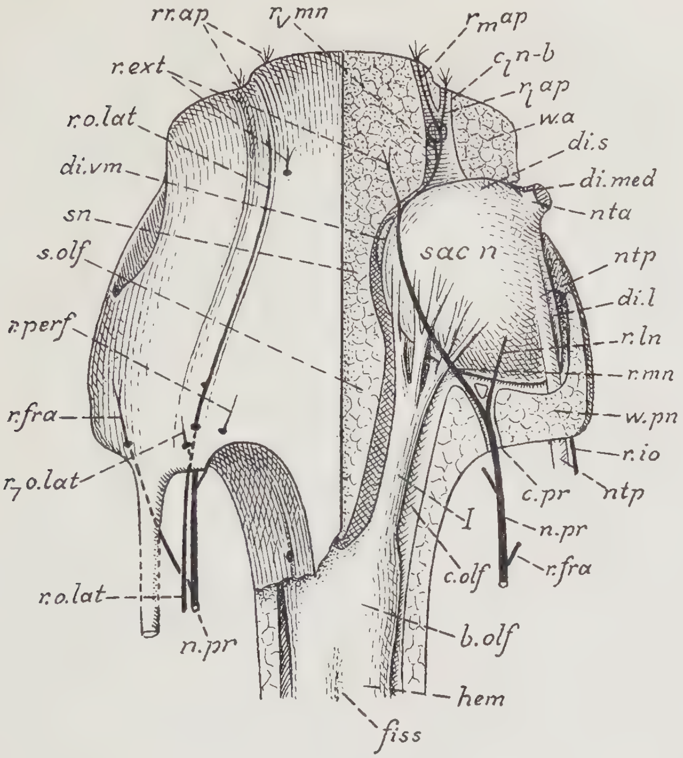

Fig. 59. *Eusthenopteron foordi* Whiteaves. Restoration of the nasal sac, the anterior parts of the brain and certain of the nerves in their position in relation to the endocranial parts of the snout. Dorsal aspect. Certain upper parts of ethmosphenoid removed. $^3/_1$.

b. olf, bulbus olfactorius; $c_l n\text{-}b$, lateral branch of nasobasal canal; *c. olf,* canalis olfactorius; *c. pr,* profundus canal; *di. l, di. med,* diverticulum laterale and medium of nasal sac; *di. s,* saccus superior of nasal sac; *di. vm,* ventro-medial diverticle of nasal sac; *fiss,* fissura sagittalis; *hem,* forebrain hemisphere; *n. pr,* n. profundus; *nta,* anterior external nasal tube; *ntp,* posterior external nasal tube (nasolachrymal duct); *r. ext,* r. externus narium of n. profundus; *r. fra,* r. frontalis anterior of n. profundus; *r. io,* r. infraorbitalis of r. maxillaris V; $r_l ap$, $r_m ap$, lateral and medial terminal branches of r. medialis narium; *r. ln, r. mn,* r. lateralis and medialis narium of n. profundus; *r. o. lat,* r. ophthalmicus lateralis; *r. perf,* r. frontalis perforans of n. profundus; *rr. ap,* rami apicales; $r_v mn$, ventral terminal branch of r. medialis narium; $r_7 o.\,lat$, branch of r. ophthalmicus lateralis to canal organ in nasal 7; *sac n,* nasal sac; *sn,* septum nasi; *s. olf,* median septum between canales olfactorii; *w. a,* prenasal wall; *w. pn,* postnasal wall; *I,* n. olfactorius.

oral side of the palate to the anterior part of the pit *fo. m. obl* on the postero-ventro-medial part of the posterior face of the postnasal wall. This canal is formed when the palatoquadrate is in its natural connection with the endocranium by the vertical groove *gr. a. obl* (fig. 54; p. 452) in the foremost end of the pars autopalatina and the postnasal wall ventrally to the pit *fo. m. obl.* It is thus bounded postero-laterally by the groove *gr. a. obl* and seems to have given passage to a branch of the a. palatina which supplied the oblique muscles of the eye (see p. 547).

The knowledge now gained of the course and extent of the numerous canals, passages, grooves, etc., enables us to draw the following conclusions concerning the development of the nervous system of the snout (figs. 59—61; cf. the comparison with *Rana*, pp. 540—546).

The r. ophthalmicus lateralis (*r. o. lat*, fig. 59) left the orbit through the canal *c. o. lat*, in which it gave off a dorsal branch ($r_7o.\,lat$) to a sensory canal organ in the nasal 7. After emerging through the probable anterior orifice of the canal *c. o. lat* it seems to have passed forwards in the groove *gr. soc* between the ethmoidal region and the ethmoidal shield. During this part of its course it gave off branches to the sensory canal organs in the six anterior nasals.

The n. profundus (*n. pr*, figs. 59, 61) was not particularly strongly developed (cf. p. 376). While still in the anterior part of the orbit it seems to have given off two branches, one posterior lateral and one anterior medial. The lateral one, the r. frontalis anterior (*r. fra*), went antero-dorsolaterally through the canal *c. fra* in the postnasal wall to the posterolateral parts of the snout behind the fenestra exonarina anterior. The medial branch, the r. frontalis perforans (*r. perf*), traversed the canal *c. perf* in the postnasal wall and went to the postero-medial dorsal parts of the snout. The n. profundus left the orbit through the profundus canal (*c. pr*), through which it reached the nasal cavity. Already within the profundus canal it broke up into two main branches, a lateral one, the r. lateralis narium, and a medial one, the r. medialis narium. The r. lateralis narium (*r. ln*) seems to have gone dorsally to the posterolateral part of the nasal sac in a direction anteriorly and laterally towards the fenestra endonarina anterior. The r. medialis narium (*r. mn*) passed forwards and somewhat medially above both the n. olfactorius and the postero-medial part of the nasal sac to the antorior part of the septum nasi. Along this part of the septum nasi it continued in a direction forwards and downwards in the groove *gr. mn* close behind the medial part of the crista intermedia (*cr. im*) on the anterior face of the nasal cavity. Just behind the medial end of the crista intermedia it gave off a branch, the r. externus narium (*r. ext*), which through the canal *c. ext* ascended to the antero-medial dorsal parts of the snout. Below the crista intermedia the r. medialis narium went downwards and forwards through the medial part of the recessus inferior, after which it left the nasal cavity through the nasobasal canal (*c. n-b*). Within that canal it gave off a strong ventral terminal branch (r_vmn, figs. 59—61) which went down to the prenasal pit and the fossa apicalis through the ventral branch of the nasobasal canal ($c_v\,n\text{-}b$). The branch

$r_{v}mn$ may have joined the medial terminal branch of the r. palatinus VII (see p. 480) to form a prenasal anastomosis (*ast.pren*), further discussed below (p. 480). After giving off the ventral terminal branch the remainder of the r. medialis narium bifurcated into a medial ($r_{m}ap$) and a lateral ($r_{l}ap$) terminal branch. These two branches went forwards through the medial ($c_{m}n$-b) and lateral ($c_{l}n$-b) terminal branches of the nasobasal canal and broke up in front of these canals into several fine twigs, the rr. apicales (*rr.ap*, figs. 59—61), which entered the naso-rostro-premaxillary (cf. $f.\,ap_{m}$, $f.\,ap_{l}$, fig. 68 D; cf. also pp. 504—505).

The r. maxillaris V (*r.mx*, fig. 61) seems to have entered the orbit together with the r. mandibularis V through the distinct incisure (*i. V*, pl. 10; cf. also Holmgren and Stensiö 1936, fig. 270 A, *V*) behind the processus ascendens in the dorsal margin of the palatoquadrate (cf. pl. 10; *asc.pq*). Soon afterwards it must have gone in an antero-ventro-lateral direction towards the lateral (lower) margin of the palatoquadrate, and during this part of its course it probably divided into the following four main branches: 1) The r. infraorbitalis (*r.io*, figs. 59—61). This branch first went forwards through the orbit, thence conceivably continuing to the nasal cavity through the fenestra endonarina posterior. Within the nasal cavity it presumably lay above the diverticulum laterale of the nasal sac close to the nasolachrymal duct and close medially to the lateral nasal wall. It may have terminated somewhere near the fenestra exonarina anterior. 2) The postchoanal anastomosis (*ast.pch*, figs. 60, 61). This branch traversed the canal *c.ast* in the dermopalatine, after which it went antero-medially across the antero-medial part of the dermopalatine, close below and about parallel to the thick postero-lateral part of the ventral margin of the postnasal wall and along the very antero-lateral margin of the pars autopalatina of the palatoquadrate. At the notch *i.ast* in the medial margin of the dermopalatine, that is to say posteriorly to the foremost free end of the dermopalatine and close antero-laterally to the anterior end of the pars autopalatina, it turned downwards to the lower side of the dermopalatine. Here it went postero-medially in the groove $gr_{2}ast$ and passed over into the r. palatinus VII. An anterior branch (*r.vot*) from the postchoanal anastomosis may have supplied the tusks and possibly also the other teeth of the vomer through the canal *c.vot*. 3) The r. palatonasalis (*r.p-n*, figs. 60, 61). This branch, which may have been a branch from the postchoanal anastomosis (cf. pp. 330, 543), passed forwards through the posterior ($c_{p}p$-n) and anterior ($c_{a}p$-n) palatonasal canals to the prenasal pit and the fossa apicalis (pp. 473—474). Between the opening *f.buc* and the anterior palatonasal canal it probably lay laterally to the choana in the mucous membrane which covered the medially curved ventral part (*w.lic*) of the lateral

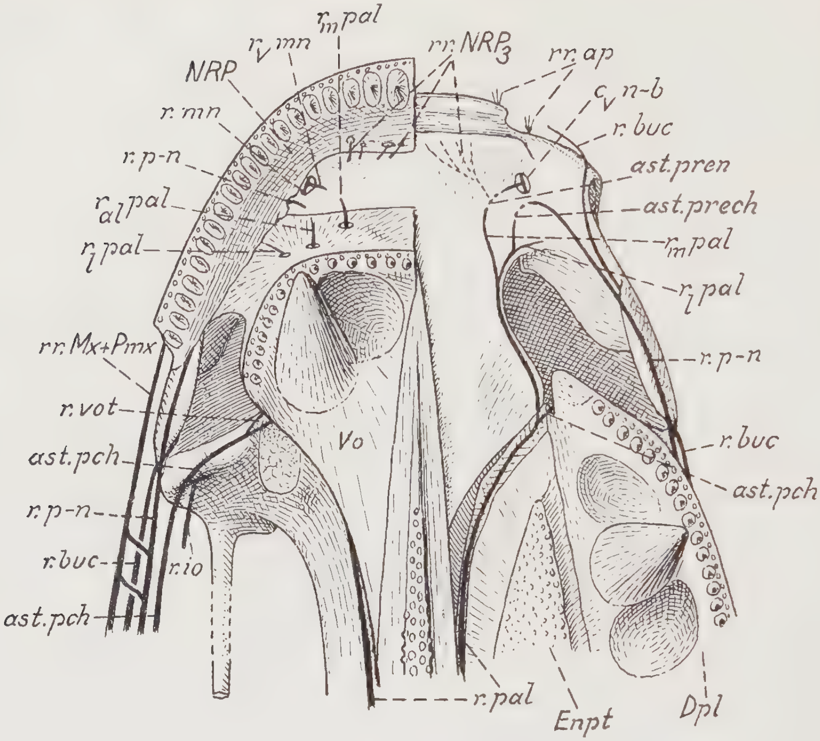

Fig. 60. *Eusthenopteron foordi* Whiteaves. Restoration showing certain of the cranial nerves of the snout in their relation to the anterior parts of the divisio cranialis anterior and the palatoquadrate complex. Palatoquadrate complex of right side and vomer and naso-rostro-premaxillary of left side removed. $^3/_1$.

Dpl, dermopalatine; *Enpt,* entopterygoid; *NRP,* naso-rostro-premaxillary; *Vo,* vomer; *ast. pch, ast. prech, ast. pren,* postchoanal, prechoanal, and prenasal nerve anastomoses; c_v*n-b,* ventral branch of nasobasal canal; r_{al}*pal,* antero-lateral terminal branch of r. palatinus VII; *r. buc,* r. buccalis lateralis; *r. io,* r. infraorbitalis of r. maxillaris V; r_l*pal,* r_m*pal,* lateral and medial terminal branches of r. palatinus VII; *r. mn,* r. medialis narium of n. profundus; *r. pal,* r. palatinus VII; *r. p-n,* r. palatonasalis; *rr. ap,* rr. apicales of the lateral and medial terminal branches of r. medialis narium; *rr. Mx + Pmx,* branches, probably of r. palatonasalis, innervating maxillary and premaxillary teeth; *rr. NRP*$_3$, branches, probably of prenasal anastomosis, supplying pars palatina of naso-rostro-premaxillary; r_v*mn,* ventral terminal branch of r. medialis narium; *r. vot,* branch of postchoanal anastomosis, innervating vomerine tusks and teeth.

nasal wall. The branch in question may have given off fine lateral branches (*rr. Mx + Pmx*) which after entering the longitudinal canal in the maxillary and premaxillary (*c. Mx, c. Pmx*) passed down to the teeth of the maxillary and premaxillary. 4) The rr. cutanei maxillares. These branches seem to have gone to an area ventrally to the eye. That they actually existed is proved by the fact that the ectopterygoid, dermopalatine, lacrymal, and maxillary present several fine canals and grooves which must have been developed for cutaneous nerves and vessels. Some

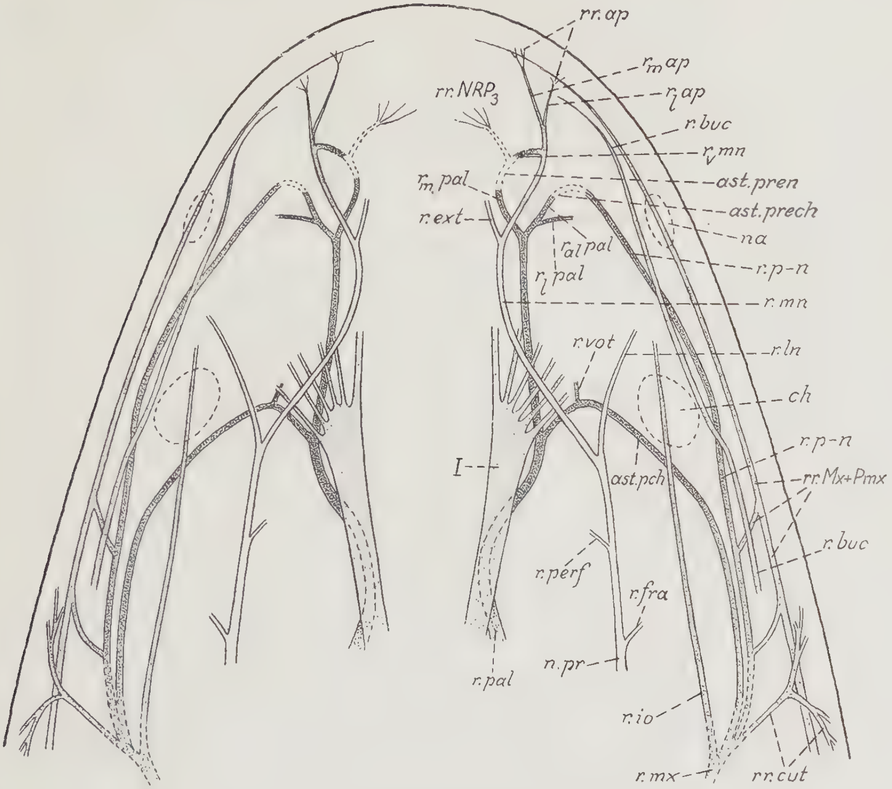

Fig. 61. *Eusthenopteron foordi* Whiteaves. Diagram of the cranial nerves of the snout in dorsal view. The most dorsal nerves are unshaded, whereas the others are shaded to a different degree according to their relative position from above downwards. The r. ophthalmicus lateralis omitted. $^7/_2$.

ast.pch, ast.prech, ast.pren, postchoanal, prechoanal, and prenasal nerve anastomoses; *ch,* choana; *na,* anterior external nostril; *n.pr,* n. profundus; $r_{al}pal$, antero-lateral terminal branch of r. palatinus VII; *r.buc,* r. buccalis lateralis; *r.ext,* r. externus narium of n. profundus; *r.fra,* r. frontalis anterior of n. profundus; *r.io,* r. infraorbitalis of r. maxillaris V; r_lap, r_map, lateral and medial terminal branches of r. medialis narium; *r.ln, r.mn,* r. lateralis narium and r. medialis narium of n. profundus; r_lpal, r_mpal, lateral and medial terminal branches of r. palatinus VII; *r.mx,* r. maxillaris V; *r.pal,* r. palatinus VII; *r.perf,* r. frontalis perforans of n. profundus; *r.p-n,* r. palatonasalis; *rr.ap,* rr. apicales; *rr.cut,* rami cutanei maxillares; *rr.Mx+Pmx,* probable branches of r. palatonasalis, innervating the teeth of the maxillary and premaxillary; $rr.NRP_3$, branches, probably of prenasal anastomosis, supplying pars palatina of naso-rostro-premaxillary; r_vmn, ventral terminal branch of r. medialis narium; *r.vot,* branch of postchoanal anastomosis innervating vomerine tusks; *I,* n. olfactorius.

of these canals and grooves indicate that certain of the nerves and vessels must have passed backwards.

The r. buccalis lateralis (*r.buc,* figs. 60, 61) was well developed and reached forwards to the very rostral part of the snout. In the middle ventral part of the orbit it gave off a branch through the canal c_{La_2}*buc* to a sensory canal organ in the middle part of the lachrymal. It left the orbit at the antero-latero-ventral corner through the opening *f. buc* just latero-ventrally to the postero-ventral process (*pr. pv*) of the ethmoidal region. Immediately in front of the opening *f. buc* it sent off a branch to a sensory canal organ in the foremost part of the lachrymal, after which it entered the lateral recess of the nasal cavity through the notch *i. buc* in the postero-ventral corner of the lateral nasal wall. Within the lateral recess the nerve went forwards laterally to the choana and ventrally to the diverticulum laterale of the nasal sac. In front of that it passed forwards in the canal *c. buc*, first immediately underneath the lamina nariochoanalis and then further anteriorly along the ventro-lateral margin of the ethmoidal region. Underneath the lamina nariochoanalis it gave off a branch through the canal $c_{R.l}$*buc* to a sensory canal organ in the lateral rostral. In its foremost part it gave off at least one branch to sensory canal organs in the medial rostral.

The r. palatinus VII (*r. pal*, figs. 60, 61) went forwards in the roof of the mouth along the parasphenoid, ventro-medially to the toothless medial marginal area of the entopterygoid, to the palatine canal (*c. pal*). Just before entering this canal it gave off a lateral branch, which joined a branch of the r. maxillaris V to form the postchoanal anastomosis (*ast. pch*). During its passage through the palatine canal it pierced the vomer from the dorsal to the ventral face and broke up into three terminal branches, a medial (r_m*pal*), an antero-lateral (r_{al}*pal*) and a lateral one (r_l*pal*), all of which emerged in the prenasal pit in the lateral part of the fossa apicalis. The medial branch had its exit fairly close to the exit of the ventral terminal branch (r_v*mn*) of the r. medialis narium in the prenasal pit and it is probable that these two nerves actually passed over into each other, forming a prenasal anastomosis (*ast. pren*). It is also probable that another anastomosis, the prechoanal anastomosis (*ast. prech*), was developed between the antero-lateral terminal branch of the r. palatinus and the r. palatonasalis (*r. p-n*). The prenasal anastomosis probably gave off an anterior branch which broke up into several fine twigs (*rr.* NRP_3) and through the canals *c.* NRP_3 entered the pars palatina of the naso-rostro-premaxillary.

The data on the nervous system thus show that the n. profundus was not very strongly developed and did not supply the lateral parts of the snout. On the other hand both the r. maxillaris V and the r. buccalis lateralis were well developed and extended far forwards towards the tip of the snout. The lateral parts of the snout were innervated by the r. maxillaris V.

With the exception of the probable vascular canals *c. ca*, *c. cut. va* and *c. a. obl* described above (pp. 469—470, 474—476) the snout seems to be devoid of canals, openings or grooves transmitting vessels only. It is obvious, therefore, that all larger vessels to and from the snout must have accompained the nerves. From this it follows that the lateral parts of the ethmoidal region both received their blood-supply and were drained by vessels which passed along the r. palatonasalis of the r. maxillaris V and the r. buccalis lateralis and which entered and left the orbit through the opening *f. buc.*

b. Remarks on other Osteolepiformes.

After the exhaustive account of *Eusthenopteron foordi* we shall now enter briefly upon the development of the snout in other Osteolepiform Crossopterygians, turning first to the species *Eusthenopteron säve-söderberghi* Jarvik and *E. wenjukowi* (Rohon) already dealt with by the present writer in 1937.

The divisio cranialis anterior chosen as a holotype of *E. säve-söderberghi* lacked the foremost part of the snout in 1937. The missing part has now been found and thus certain addenda can be made to my previous description. It is now obvious that the snout of *E. säve-söderberghi* (fig. 62 A) is actually longer and narrower than in the restorations made in 1937 (Jarvik 1937, figs. 6, 8). The divisio prenasalis communis (*w. pren*) is both longer and, anteriorly, narrower than in *E. foordi*. The fossa apicalis (*fo. ap*) is not quite twice as broad as long, whereas in *E. foordi* (figs. 56, 87 A; pl. 8, fig. 1) it is almost three times as broad as long. The anterior palatal fenestra (*fe. pal*) is also longer and narrower than in *E. foordi* and, contrary to conditions in that species, divided posteriorly into right and left halves by a strong median anterior process ($pr_m Vo$) from the two vomers.

As previously shown (Jarvik 1937, p. 72; figs. 4 B, 8), the lamina supraorbitalis in *E. säve-söderberghi* is divided by a deep notch in its posterior margin into two supraorbital processes, the processus supraorbitalis lateralis and the processus supraorbitalis medialis. Only the lateral one is developed in *E. foordi*, where the medial supraorbital process is represented by the part of the lamina supraorbitalis (*la. so*, fig. 47) that lies medially to the groove *gr. soc.* If this groove were deepened posteriorly so as to form a notch in the posterior margin of the lamina supraorbitalis, a process would arise medially to the notch, in all respects resembling the processus supraorbitalis medialis in *E. säve-söderberghi.*

E. wenjukowi (Jarvik 1937, pp. 90—108, figs. 10—16) is both as to the general shape of the snout and the shape and development of the fossa apicalis almost exactly as *E. foordi*. The crista suspendens is, however, more strongly developed and does not issue from the thin ventral part of the interorbital wall but higher up, from the ventro-lateral part of the olfactory ridge. The pit (JARVIK 1937; *p*, figs. 10, 11, 13, 14 A, 15) which corresponds to the pit *fo. pr. dm* in *E. foordi* (figs. 47 B, 48—50) is strongly developed. On the part of the posterior face of the postnasal wall that corresponds to the area situated just around the posterior orifice of the profundus canal in *E. foordi* (*c. pr*, figs. 49, 50) there is a pit in *E. wenjukowi* (the orbitonasal pit, JARVIK 1937, p. 97; *on. p*, figs. 12, 13), at the bottom of which are several (4—5) foramina. The opinion advanced by the writer in 1937 that this pit may have been the area of origin of the oblique eye muscles is untenable. The presence of several foramina at the bottom of the pit may simply imply that the vessels which accompanied the n. profundus pierced the postnasal wall through separate canals. Besides, it is also possible that the n. profundus broke up into its lateral and medial narial branches just before its entrance into the postnasal wall and that consequently there were separate canals for these two branches. Finally, it should be mentioned that the anterior palatonasal canal in *E. wenjukowi* is well developed (JARVIK 1937, p. 93) and traverses the prenasal wall. In *E. foordi* the corresponding canal (pp. 473—474) passes between the endocranium and the dermal bones below.

In other forms, placed by WOODWARD (1932, pp. 110—112) in the family *Rhizodontidae*[1], the structure of the snout is still very imperfectly known. The endocranium of *Rhizodopsis sauroides*, which was described and figured by SÄVE-SÖDERBERGH (1936, pp. 136—142; figs. 58, 59), agrees essentially with that of *Eusthenopteron foordi*. The ethmoidal region seems to be comparatively short and high. The postnasal wall is pierced by a canal (SÄVE-SÖDERBERGH 1936; *onc*, fig. 58), which on account of its position must represent the profundus canal in *Eusthenopteron* (*c. pr*, figs. 49, 50). The posterior face of the postnasal wall has at least one articular area (*ca*) for the palatoquadrate, which seems to correspond to the medial autopalatine articular area (*art*$_1$*m*) in *Eusthenopteron.* Also the external orifice of the canal for the v. cerebralis anterior (*v. c. a.*) is situated as in that form. In their description of the dermal bones WATSON and DAY (1916, p. 13) state that they have noticed a "small process rising from the anterior end of the maxilla, whose anterior border forms a rounded margin which can only be that of an external nostril". As shown above (p. 454), the maxillary of *Eusthenopteron* is provided with a similar dorsal process (*pr. Mx*, fig. 68 A) bounded by a concave anterior margin, which, however, has no relations to the external nostril. The presence of this process, the very similar disposition of the dermal bones in general (TRAQUAIR 1881; WATSON and DAY 1916), and the great agreement in the development of the endocranium definitely indicate that *Rhizodopsis* and *Eusthenopteron* must be closely allied. The other forms placed by WOODWARD in the *Rhizodontidae*[1] are very slightly known, but at least *Tristichopterus* (JARVIK 1937, pp. 64—68) and *Sauripterus* may have resembled *Eusthenopteron.*

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[1] The family *Rhizodontidae* as hitherto defined by WOODWARD and most other writers was recently subdivided by BERG (1940, p. 389) into two families, *Rhizodontidae* s. str. and *Rhizodopsidae*. According to BERG the clavicle is provided with an ascending process in *Rhizodontidae* (*Rhizodus, Strepsodus*), but is devoid of this process in *Rhizodopsidae*. The process in question is, however, as I have been able to establish, present in *Eusthenopteron*, which is placed by BERG in the family *Rhizodopsidae*, and probably also in the genus *Rhizodopsis* itself (sp. No. P. 7557, British Museum N. H., London). In these circumstances the two families *Rhizodontidae* Berg and *Rhizodopsidae* Berg can of course not be accepted. Also in *Porolepis, Glyptolepis* and *Laccognathus* ("*Dendrodus*"; GROSS 1936, figs. 1, 3; cf. pp. 153—154 and GROSS 1941, p. 19) among the *Porolepiformes* the clavicle has an ascending process. The presence of this process thus seems to be a character common to all Rhipidistid Crossopterygians. It may be added here that the subdivisions of the families *Osteolepidae* and *Coelacanthidae* suggested by BERG (1940, pp. 388—392) are also based on insufficient grounds and thus they cannot either be adopted here.

Among the forms included by WOODWARD (1932, p. 110) in the *Osteolepidae* the endocranium is known in *Osteolepis* (WATSON 1926) and *Ectosteorhachis* ("*Megalichthys*", ROMER 1937; cf. ROMER 1941, p. 142), but has been described in detail only in the latter form. The ethmoidal region in *Ectosteorhachis* in several respects strongly reminds of that in *Eusthenopteron.* The nasal cavities are separated by a median septum which on either of its lateral faces bears a "pocket" (ROMER 1937, p. 22; fig. 2, *ncm*) forming a ventro-medial recess of the nasal cavity (cf. p. 466). This recess was considered by ROMER to have lodged a structure probably representing Jacobson's organ, an opinion which is supported by the studies now carried out (cf. p. 536). The canalis olfactorius (ROMER 1937, figs. 8—10) is as in *Eusthenopteron* (fig. 57 A—C), with the difference, however, that it is separated from the corresponding canal of the opposite side backwards as far as to the pituitary fossa. This means that in its posterior part it must have lodged the hemisphere and the bulbus olfactorius of its side. Thus neither of these portions of the brain lay close to the corresponding ones of the opposite side, as they did in *Eusthenopteron* (fig. 59), but were separated from them practically throughout their extent. From the anterior part of the canalis olfactorius issue several branching canals (ROMER 1937, p. 32; figs. 8—10) upwards towards the dermal bones. These canals correspond to the canal *c. cut. va* (p. 469 above and fig. 57) and its branches in *Eusthenopteron.* The canals

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[1] *Euporosteus* has turned out to be a Coelacanthid (STENSIÖ 1937 a) and *Dictyonosteus* conceivably also belongs among the Coelacanthids (see p. 579). According to WESTOLL (1936, p. 167), the genus *Gyroptychius* includes different Osteolepids in which the cosmin layer of the exoskeleton is reduced.

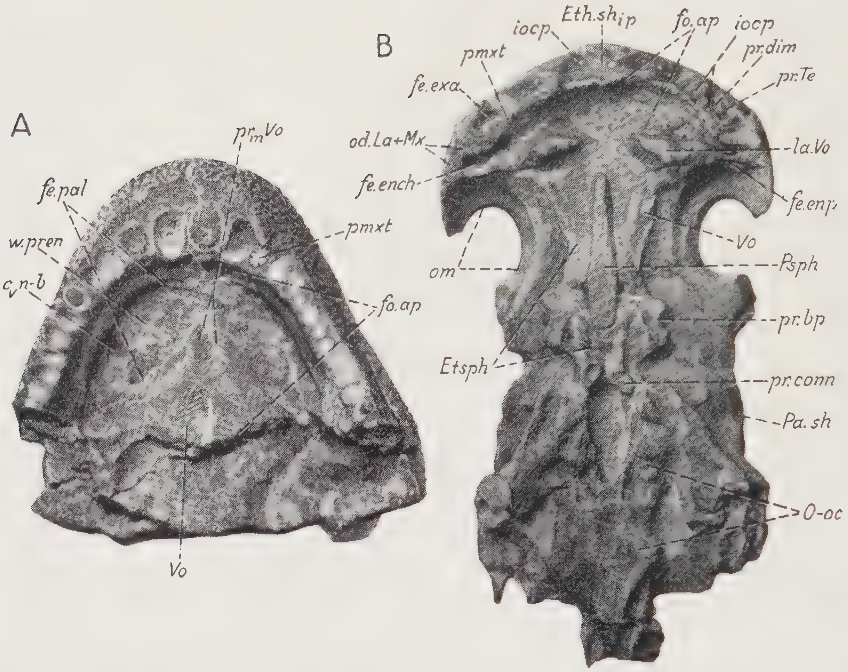

Fig. 62. A, *Eusthenopteron säve-söderberghi* Jarvik. Foremost part of the snout of the holotype. Ventral view. $^{8}/_{3}$. B, *Thursius?*, dorso-ventrally flattened cranium in ventral view. Specimen No. 53397 in the Geological Survey, London, figured in dorsal view by JARVIK in 1937 (fig. 18). $^{4}/_{3}$.

Eth. sh$_{ip}$, compressed part of ethmoidal shield; *Etsph*, ethmosphenoid; *O-oc*, otico-occipital; *Pa. sh*, parietal shield; *Psph*, parasphenoid; *Vo*, vomer; *c*$_v$*n-b*, ventral branch of nasobasal canal; *fe. exa*, fenestra exonarina anterior; *fe. ench*, fenestra endochoanalis; *fe. enp*, opening in postnasal wall, probably representing fenestra endonarina posterior; *fe. pal*, anterior palatal fenestra; *fo. ap*, fossa apicalis; *iocp*, pores of infraorbital sensory canal; *la. Vo*, vertical tooth-bearing lamina of vomer; *od. La+Mx*, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *om*, margin of orbital opening; *pmxt*, premaxillary teeth; *pr. bp*, basipterygoid process; *pr. conn*, processus connectens; *pr. dim*, processus dermintermedius of lateral rostral; *pr. Te*, process, probably of anterior tectal, extending into nasal cavity; *pr*$_m$*Vo*, anterior median process of vomers; *w. pren*, divisio prenasalis communis.

for the r. ophthalmicus lateralis and n. profundus (ROMER 1937, p. 32; figs. 8, 10, *VIIos2*, *onc*) were also very much as in *Eusthenopteron* (pp. 470, 471; *c. o. lat*, *c. pr*, figs. 49, 50, 57 A—C), and quite as in that form the r. medialis narium went forwards in a groove in the anterior part of the septum nasi (ROMER 1937, p. 32; cf. *gr. mn*, figs. 47 B, 57 A in the present work). In that groove the r. medialis narium gave off an antero-medio-dorsal branch corresponding to the r. externus narium in *Eusthenopteron* (p. 476; *r. ext*, figs. 59, 61) and strictly homologous to the r. externus narium in *Rana* (p. 542). The canal for this branch (*c. ext* in *Eusthenopteron*; p. 470; figs. 47 A—C, 57 B—D; *cfa* in *Ecto-*

steorhachis; ROMER 1937, p. 32; fig. 8) thus cannot be the equivalent of the fenestra nasobasalis (fen. apicalis) in *Rana* (*fe. nb*, fig. 22 B, C), as maintained by ROMER, but must represent instead the foramen frontale (*f. fr*, figs. 22 B, C, 29, 30). Whether there is any canal in *Ectosteorhachis* corresponding to the canalis nasobasalis in *Eusthenopteron* (p. 470) is unknown. The lateral parts of the ethmoidal region do not seem to have been ossified in the *Ectosteorhachis* specimens studied by ROMER (cf. ROMER 1941). The lamina nariochoanalis probably consisted entirely of cartilage, which was sometimes the case also in *Eusthenopteron* (p. 427).

In three specimens of Osteolepids, which according to the accompanying labels belong to the genera *Osteolepis*, *Thursius?* (fig. 62 B) and *Diplopterax* (fig. 63)[1], it is clearly seen that the dermal bone — in all probability the lateral rostral — that forms the ventral boundary of the fenestra exonarina anterior (*fe. exa*) is provided with a strong process (*pr. dim*) which extends far medially into the nasal cavity and undoubtedly is a processus dermintermedius homologous to that in *Eusthenopteron* (p. 449; figs. 68 A, 70 A; pl. 6, fig. 2). The presence of this process indicates that also a processus intermedius must have been developed. At any event it is quite clear that the antero-lateral part of the nasal cavity was subdivided into compartments on the whole in the same way as in *Eusthenopteron*. At least in *Thursius?* and *Diplopterax* the dermal bone — conceivably the anterior tectal — that forms the posterior part of the upper margin of the fenestra exonarina anterior bears a process directed inwards (*pr. Te*, figs. 62 B, 63), which corresponds exactly to the similarly directed process of the anterior tectal (*pr. Te*, p. 448; cf. fig. 52 B; pl. 9, fig. 1) in *Eusthenopteron*.

The fenestra exonarina anterior (*fe. exa*) in *Osteolepis macrolepidotus* (see SÄVE-SÖDERBERGH 1933 a, figs. 19 A, B, 20 A, B; 1941, figs. 2 A, B, 3 A, B, 8) has a position approximately as in *Eusthenopteron* (fig. 68 A; pl. 6, figs. 1, 2), whereas in *Thursius?* (fig. 62 B) and *Diplopterax* (fig. 63) it seems to lie a little further caudally, i. e. somewhat nearer the postero-ventro-lateral corner of the ethmoidal shield. GOODRICH (1909, p. 280; 1919, p. 184; 1928, p. 90) and WESTOLL (1937 a, p. 28; cf. MOY-THOMAS 1939 a, p. 79) state that in certain Osteolepids the fenestra is situated at the very ventral border of the ethmoidal shield, and WESTOLL expresses himself as follows: "in early forms (e. g., *Thursius*, *Diplopterax*) the external and internal nares may be confluent, the former being merely notches in the dermal bones of the lip". In the specimens of *Thursius?* and *Diplopterax* figured here (figs. 62 B, 63) this is not the case. The fenestra in question has both in these and in *Osteolepis* the same position in relation to the lower margin of the ethmoidal shield as in *Eusthenopteron*. This seems to be so also in Osteolepids in general, according to my preparations of several specimens of various Osteolepids.

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[1] These three specimens are: 1) No. A. 6010, Sedgwick Museum, Cambridge, labelled *Osteolepis macrolepidotus*; 2) No. 53397, Geol. Survey, London, labelled *Thursius?* (cf. JARVIK 1937, p. 114; fig. 18); and 3) No. L. 8444, University Museum, Manchester, labelled *Diplopterus* sp. (*Diplopterax*; cf. SÄVE-SÖDERBERGH 1933 a, p. 104).

The specimen of *Thursius?* repeatedly referred to above (foot-note 1 on p. 485) was prepared from the lower side (fig. 62 B) so that the entire lower face of the cranium was made available for investigation. The ethmoidal region in this specimen, though badly crushed and damaged, is clearly of a general type similar to that in *Eusthenopteron* (cf. figs. 48—50) and this applies also to the fenestra endonarina posterior and the fenestra endochoanalis. The fenestra endonarina posterior (*fe. enp*) is thus a large opening in the ventro-lateral part of the postnasal wall and leads from the nasal cavity backwards to the anterior ventro-lateral part of the orbit. It is bounded below by a bridge of bone from the fenestra endochoanalis (*fe. ench*). The latter fenestra is large and occupies a considerable part of the solum nasi. The dermal bones covering the ventral face of the ethmoidal region are also developed much in the same way as in *Eusthenopteron* (fig. 56) and as in that form there is a fossa apicalis (*fo. ap*). The vomer (*Vo*) is provided with a tooth-bearing lamina (*la. Vo*) which enters into the posterior boundary

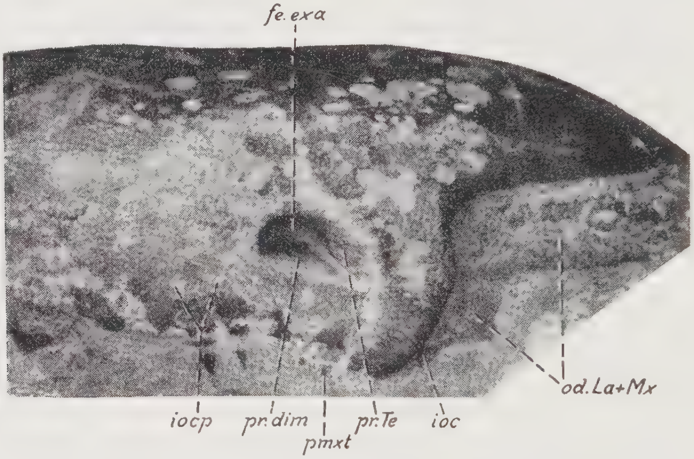

Fig. 63. *Diplopterax* sp. Part of the fronto-ethmoidal shield, showing the fenestra exonarina anterior of the left side. Antero-lateral view. Sp. No. L. 8444, University Museum, Manchester. $^6/_1$.

fe. exa, fenestra exonarina anterior; *ioc*, infraorbital sensory canal; *iocp*, pores of infraorbital canal; *pmxt*, premaxillary teeth; *pr. dim*, processus dermintermedius; *pr. Te*, process, probably of anterior tectal, extending into nasal cavity; *od. La + Mx*, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary.

of the fossa apicalis. In the roof of this fossa there was no doubt also an anterior palatal fenestra (*fe. pal*), the exact boundaries of which cannot, however, be established. In the lateral part of the fossa apicalis there is a comparatively wide foramen corresponding to the ventral orifice of the ventral branch ($c_v n$-*b*, figs. 48, 56) of the canalis nasobasalis in *Eusthenopteron* and indicating the presence of a canalis nasobasalis in the form now under consideration. The intervomerine canal connecting the posterior part of the fossa apicalis with the dorsal part of the mouth cavity next behind the transverse parts of the tooth-bearing laminae of the vomers is also developed, but consists of a comparatively large opening, and is thus much shorter and wider than in *Eusthenopteron* (p. 459; *c. iv*, figs. 56, 58 A, 87 A). Also in the *Osteolepis* specimen dealt with above (see foot-note 1 on p. 485) the intervomerine canal was obviously developed as a wide foramen.

The above brief comments show that the Osteolepids in general agree fundamentally with *Eusthenopteron* and other Rhizodontids with regard to the development of the snout. The presence of a well developed processus dermintermedius proves that the nasal cavity was subdivided antero-laterally into a recessus superior and a recessus inferior, quite as in *Eusthenopteron*. There appears also to have been a small recessus medius. The fenestra endonarina posterior, the fenestra exonarina anterior, and the fenestra exochoanalis are both in shape and position fundamentally as in *Eusthenopteron*. The course of the n. profundus was very much as in *Eusthenopteron* and this probably applied to the other nerves as well as to the main vessels of the snout. Also in the disposition of the dermal bones of the ethmoidal shield (*Diplopterax*, "*Megalichthys*", Holmgren and Stensiö 1936, fig. 272 A, C; *Osteolepis*, Westoll 1936) and in the pattern of the dermal bones of the head on the whole (*Glyptopomus*, Watson and Day 1916; *Osteolepis*, Goodrich 1919; Swinnerton 1923; Säve-Söderbergh 1933a; 1941; "*Megalichthys*", Watson 1926, figs. 37, 38; Moy-Thomas 1935) points of great agreement are observed between *Eusthenopteron* and the Osteolepids.

Our present knowledge of Osteolepids and Rhizodontids definitely indicates that they are very closely akin. They constitute together a natural group for which the term *Osteolepiformes*[1] has been adopted in this work. It will be shown below that this group differs in several important characters from the other groups of Crossopterygians.

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[1] This term was used by Berg (1940) in a more restricted sense, viz. for the family *Osteolepidae* (cf. foot-note 1 on p. 482).

2. Comparative section.

a. Comparison with Porolepiformes.

In the comparison of the snout in *Eusthenopteron* and *Porolepis* I shall first turn to the points of agreement. Above all it then deserves to be emphasized that the walls of the nasal cavity in both *Eusthenopteron* (figs. 47, 48) and *Porolepis* (fig. 40) are pierced by three openings for nasal tubes, viz. the fenestra endonarina anterior (*fe. ena*), the fenestra endonarina posterior (*fe. enp*) near the postero-ventro-lateral corner of the nasal cavity, and the fenestra endochoanalis (*fe. ench*). Thus both forms had a true choana opening ventrally into the mouth cavity. In this respect, therefore, they were as Tetrapods. Both in *Eusthenopteron* (pp. 441, 536; figs. 51, 57) and *Porolepis* (pp. 368, 402; figs. 39, 40 A, C, 42 A—C) the nasal cavity has a lateral recess (*re. l*) which posteriorly is in open communication with the mouth cavity and shows that, quite as in Amphibians, there was a sinus lateralis nasi close dorso-laterally to the choana, continued backwards by a sulcus maxillo-palatinus. Another Amphibian character common to both forms is that the n. profundus broke up into one medial and at least one lateral nasal branch. Both *Eusthenopteron* and *Porolepis* in all probability had an intermaxillary gland (pp. 400, 505—506). The pars autopalatina of the palatoquadrate in *Porolepis* (p. 357; cf. pp. 386—387, 412—413) is imperfectly known. It is obvious, however, that it was well developed and, as the corresponding part of the palatoquadrate in *Eustenopteron* (pp. 451—453; fig. 55), formed a complete floor of the foremost part of the orbit. The presence of two articular areas on the endocranium in *Porolepis*, the area *art. aup*? (p. 359; fig. 37 A, B) and the autopalatine fossa (p. 361; *fo. aup*, fig. 37), indicates that it probably had both an antero-lateral and an antero-medial connection with the endocranium. Of these two connections the antero-lateral one corresponds to the connection between the pars autopalatina and the lateral autopalatine articular area (art_1l, figs. 48—50) in *Eusthenopteron*, whereas the antero-medial one is comparable to the connection with the medial autopalatine articular area (art_1m), the pits *fo. cr. vm* and *fo. pr. dm* and the crista suspendens of the endocranium in *Eusthenopteron*[1]. The sensory canal system of the snout is developed in a corresponding way in *Osteolepiformes* and *Porolepiformes* (pp. 334—335) and the same applies to the general pattern of the dermal bones of the snout[1] (pp. 346—353; figs. 33, 34, 37 A, 56) and to the course of the r. ophthalmicus lateralis.

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[1] The crista suspendens (*cr. susp*) is in *Porolepis* (p. 361, fig. 37) situated on the olfactory ridge, which is also the case in *Eusthenopteron wenjukowi* (JARVIK 1937, fig. 13), while in *E. foordi* (p. 439; figs. 47 B, 48, 49) it is developed on the thin ventral part of the interorbital wall.

The remaining characters that the two forms have in common are all probably of a primitive nature. Such characters are inter alia the extensive ossification of the ethmoidal region, the fact that the ethmoidal region is co-ossified with the orbitotemporal region to form the large ethmosphenoid bone, the complete and strong development of the divisio prenasalis communis, and the fairly complete development of the nasal walls.

There are, however, very considerable differences in the development of the snout in *Osteolepiformes* and *Porolepiformes*. The most important of these differences may be briefly summarized as follows.

1) The internasal wall in *Eusthenopteron* (figs. 51, 52, 59) is narrow and forms a solid nasal septum (*sn*). The internasal wall in *Porolepis* (figs. 39, 43) is broad and lodges both the ethmoidal part (*eth. cr*) of the cranial cavity and the paired cavum internasale (*cav. in*).

2) The divisio prenasalis communis is longer and narrower in *Eusthenopteron* than in *Porolepis*. On the lateral parts of its lower face in *Eusthenopteron* (fig. 48) are a pair of shallow, ventrally open prenasal pits (*fo. pren*), situated far apart from each other; to these there is no equivalent in *Porolepis*. In *Porolepis* (figs. 36 A, 37 A), on the other hand, the divisio prenasalis communis lodges the paired and comparatively deep cava prenasalia, which form the direct anterior continuation of the cava internasalia (*cav. in*) and are situated close to each other.

3) The intermaxillary gland was in *Eusthenopteron* (p. 506) situated in the fossa apicalis underneath and slightly within the divisio prenasalis communis. The main part of the gland presumably lay in the prenasal pits. Though probably paired the gland had a single median unpaired efferent duct which passed backwards through the intervomerine canal (*c. iv*, figs. 56, 58 A) in the suture between the transverse parts of the tooth-bearing laminae of the vomers. The intermaxillary gland in *Porolepis* (pp. 400—401) occupied the cava internasalia and cava prenasalia and was thus beyond doubt a paired formation situated almost entirely within the internasal wall. It was conceivably provided with several efferent ducts which pierced the mucous membrane underneath the cavum prenasale and cavum internasale.

4) The nasal cavities are fairly close to one another in *Eusthenopteron*, whereas they lie far apart in *Porolepis* (cf. No. 1).

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[1] *Eusthenopteron* has one anterior tectal only (*Te. a*, figs. 34, 68 A) while in *Holoptychius* there are several anterior tectal elements (fig. 33). Since at least two anterior tectals have been observed in certain *Osteolepiformes* (*Osteolepis*, WESTOLL 1936, fig. 3 B) this difference, however, is certainly of little importance.

5) The lamina nariochoanalis is in *Eusthenopteron* formed by the lateral nasal wall, in *Porolepis* both by the lateral nasal wall and an adjacent part of the solum nasi.

6) *Eusthenopteron* has no equivalent to Seydel's palatal process in *Porolepis* (*pr. S*, figs. 36 A, 40 A, C, D).

7) The fenestra endonarina anterior (*fe. ena*, figs. 39 A, 40 A, C, 47 B) and the fenestra endochoanalis (*fe. ench*, figs. 36 A, 40 D, 48) are comparatively large in *Eusthenopteron*.

8) The fenestra endonarina posterior (*fe. enp*) in *Eusthenopteron* (figs. 49—51) is an opening in the postnasal wall leading backwards to the anterior ventro-lateral part of the orbit, and is separated ventrally by an endoskelatal bridge from the fenestra endochoanalis; in *Porolepis* (figs. 39 B, 40 A, C) it lies in the lateral nasal wall and is continuous ventrally with the fenestra endochoanalis.

9) No canal corresponding to the nasobasal canal (*c. n-b*, figs. 52 A, C, 57 A—C, 58) in *Eusthenopteron* exists in *Porolepis*. On the other hand the orbitorostral passage (p. 369; $gr_p or$, $c_p or$, $gr_a or$, $c_a or$, figs. 37 A, B, 39, 42, 43) and the canal *c. vl* in *Porolepis* have no equivalents in *Eusthenopteron*.

10) In *Eusthenopteron* there is a single nerve-canal (*c. ext*, figs. 47, 52 A, C, 57 B—D) leading upwards from the nasal cavity to the dorsal face of the ethmoidal region; in *Porolepis* a great many nerve-canals (*c. prt*, figs. 39, 42 A, D, E, 43) ascend from the nasal cavity to the dorsal face of the ethmoidal region, piercing the dorsal part of the medial nasal wall, the adjacent part of the prenasal wall, and the medial parts of the tectum nasi.

11) The postnasal wall is pierced in *Eusthenopteron* by a single and not particularly wide profundus canal (*c. pr*, figs. 49—51, 57 A—C, E, 59); in *Porolepis* (figs. 36 B, 37 B, 39 B, 42) by a wide medial (*c. prm*) and one or several narrower lateral profundus canals ($c_1 prl$, $c_2 prl$).

12) The nasal cavity in *Eusthenopteron* (figs. 52, 57) is subdivided anteriorly and antero-laterally into a recessus superior (*re. s*), a recessus medius (*re. med*), a recessus inferior (*re. i*) and recesses for the lateral and medial nasal muscles (*re. m. ln*, *re. m. mn*). The nasal cavity in *Porolepis* (figs. 39 A, 42) shows no signs whatever of a subdivision into such compartments. The subdivision in *Eusthenopteron* is effected by several processes and crests, viz. the processus intermedius (*pr. im*, $pr. im_h$, $pr. im_{rc}$) of the lamina nariochoanalis, the lateral horisontal ridge (*ri. lh*), the crista intermedia (*cr. im*), the processus dermintermedius (*pr. dim*, $pr. dim_{rc}$) of the lateral rostral and the inwardly directed process (*pr. Te*) of the anterior tectal. *Porolepis* is completely devoid of equivalents to these pro-

cesses and crests. The nasal cavity in *Eusthenopteron* has a ventromedial recess (*re. vm*). This recess is not developed in *Porolepis*.

13) In *Eusthenopteron* (figs. 47 B, C, 48, 51, 57) the lateral recess (*re. l*) of the nasal cavity is bounded by the medially curved ventral part (*w. lic*) of the lateral nasal wall only. In *Porolepis* (figs. 39, 46 A) it is bounded laterally by the lateral nasal wall, ventrally by the postero-lateral part of the solum nasi, and dorsally by the crista rostro-caudalis (*ri. w. al*). In *Eusthenopteron* the postero-lateral part of the solum nasi is absent. *Eusthenopteron* lacks a crista rostro-caudalis.

14) The posterior external nasal tube in *Eusthenopteron* (p. 467) went outwards to the posterior external nostril through the foremost part of the orbital opening just in front of the eye-ball and was here surrounded by soft tissue only. It lay medially to the dermal bones that form the lateral boundary of the anterior part of the orbit. In *Porolepis* (pp. 405—407) the posterior external nasal tube pierced an opening (*fe. exa*, fig. 41) in the ethmoidal shield outside the fenestra endonarina posterior. This fenestra exonarina posterior is situated on the lateral side of the snout fairly far in front of the orbital opening, about midway between that and the fenestra exonarina anterior. As it extended backwards to close in front of the eye-ball, the posterior external nasal tube in *Eusthenopteron* was transformed into a nasolachrymal duct. This was not the case with the corresponding tube in *Porolepis*.

15) The large differences in the nasal cavity show that there must have been considerable differences in the development of the nasal sac.

16) The forebrain in *Eusthenopteron* (fig. 59; cf. fig. 57 A—C) was of approximately the same breadth as the diencephalon; in *Porolepis* (fig. 43; cf. fig. 38) it was much broader than the diencephalon. The bulbi olfactorii (*b. olf*) in *Eusthenopteron* lay close to one another immediately in front of the hemispheres (*hem*), whereas in *Porolepis* they were situated far apart at the lateral sides of the hemispheres.

17) The lateral parts of the snout were in *Eusthenopteron* supplied mainly by the r. maxillaris V, in *Porolepis* mainly by the n. profundus.

18) In *Eusthenopteron* the r. buccalis lateralis (*r. buc*, figs. 60, 61) passed forwards in the pons nariochoanalis laterally to the choana, giving off branches to the neuromasts of the anterior parts of the infraorbital sensory canal. It terminated far anteriorly near the very tip of the snout. In *Porolepis* (pp. 378, 394) it presumably broke up into several terminal branches while still in the orbit. One of these terminal branches, which supplied the foremost neuromasts of the infraorbital sensory canal, went forwards through the orbitorostral passage medially to the choana.

19) The n. profundus (*n. pr*) in *Eusthenopteron* (figs. 59, 61) was com-

paratively weakly developed. It bifurcated into a lateral (*r. ln*) and a medial (*r. mn*) nasal branch, normally during its passage through the postnasal wall (cf. No. 11). The medial nasal branch traversed the nasal cavity without giving off more than one dorsal branch (*r. ext*; cf. No. 10). The n. profundus in *Porolepis* (fig. 43) was strongly developed While still in the orbit it broke up into a medial (*r. prm*), two or three lateral nasal branches (*r. prl*) and an orbitorostral branch (*r. pror*; cf. No. 11). In the nasal cavity the medial nasal branch divided into numerous dorsal branches (*rr. prt*; cf. No. 10).

20) The r. palatinus VII (*r. pal*) in *Eusthenopteron* pierced the antero-lateral part of the vomer and during this part of its course it broke up into three branches, one medial ($r_{m}pal$), one antero-lateral ($r_{al}pal$) and one lateral ($r_{l}pal$). In *Porolepis* the r. palatinus VII probably did not divide during its passage through the vomer; its canal in that bone (*c. pal* fig. 37 A), which is situated in the postero-medial part of the bone, is unbranched throughout.

21) The connections between the pars autopalatina of the palatoquadrate and the endocranium are more differentiated and more rigid in *Eusthenopteron* than in *Porolepis.* In one place in *Eusthenopteron* there was presumably a synchondrotic connection between the pars autopalatina and the endocranium (pp. 457—458), but in *Porolepis* the autopalatine articular fossae on the endocranium are lined with periostal bone indicating that there cannot have been any synchondrotic connection.

22) In *Eusthenopteron* and other *Osteolepiformes* there is found a pineal foramen between the frontals, which at least in certain forms (*Diplopterax*, *Eusthenopteron*, *Thursius*?; cf. JARVIK 1937, p. 84; figs. 4 A, 6, 18) is surrounded by small pineal plates (*Pin. pl*, fig. 34). In *Porolepiformes* there is at least as a rule no pineal foramen (cf. p. 362), though the pineal organ extended up underneath the dermal skull roof where it lay in a pit (*fo. pin*, fig. 33) on the lower side of the most posterior post-rostral plate.

23) The vomers (*Vo*) in *Eusthenopteron* (figs. 56, 87 A) meet anteriorly in a median suture but their long posterior processes ($pr_{p}Vo$) diverge and are separated from one another by the parasphenoid. Each vomer is provided with a descending tooth-bearing lamina (*la. Vo*). The vomers in *Porolepis* (fig. 37 A; cf. fig. 44) lie mainly in front of the parasphenoid. Their posterior parts are close to one another, but further anteriorly they diverge strongly. They have neither a posterior process nor a descending tooth-bearing lamina.

24) The parasphenoid (*Psph*) in *Eusthenopteron* (figs. 56, 87 A) is narrow and goes forward underneath the ethmoidal region practically to the transition between the internasal wall and the divisio prenasalis

communis. The parasphenoid in *Porolepis* (fig. 37 A; cf. fig. 44) is broad and hardly extends forwards onto the lower face of the ethmoidal region.

25) The fossa apicalis (*fo. ap*), intervomerine pit (*fo. iv*) and intervomerine canal (*c. iv*) present in *Eusthenopteron* (figs. 56, 58, 87 A) are all absent in *Porolepis* (fig. 37 A; cf. fig. 44).

26) The anterior palatal fenestra in *Eusthenopteron* (*fe. pal*, figs. 56, 87 A) is comparatively small, lies entirely in front of the vomers underneath the divisio prenasalis communis, and does not form the ventral opening of any large cavity. The anterior palatal fenestra in *Porolepis* (fig. 37; cf. fig. 44) is large, lies chiefly between the vomers underneath the internasal wall, and in it are seen the ventral openings of the cava internasalia and prenasalia.

Eusthenopteron and *Porolepis* thus present both points of agreement and differences in the development of the snout. The points of agreement must on the whole be regarded as primitive and derived from common ancestors, and some of them are also shared by the Amphibians. The differences are numerous and of so profound a nature that they plainly show that the two forms must have passed through a long development independently of one another. In these circumstances and since the snout in other Rhipidistid Crossopterygians as far as known agrees fundamentally either with that in *Eusthenopteron* or in *Porolepis*, it follows that the Rhipidistid Crossopterygians include two different lineages, and on the basis of the structure of the snout we are therefore justified in dividing the Rhipidistids into two groups, *Osteolepiformes* and *Porolepiformes*[1].

If we were to judge solely from the development of the snout, we should probably regard *Osteolepiformes* and *Porolepiformes* as fairly remote groups, which must be classified far apart. What is known at present concerning the other parts of the skull, however, manifests beyond doubt that in spite of the differences in the snout the two groups in question must be closer to one another than to any other groups (cf. p. 596 below).

The most important common characters in the skull that argue decidedly in favour of a fairly close relationship between *Osteolepiformes* and *Porolepiformes* may be briefly summarized as follows: 1) The disposition and development of the sensory canal system. 2) The pattern of the dermal bones of the skull-roof, cheek, lower jaw and opercular apparatus (see e. g. Holmgren and Stensiö 1936, figs. 273, 274, 276; Westoll 1937, fig. 1 B, C). 3) The presence of an ascending process on the clavicle (see foot-note on p. 482). 4) The fact that the endocranium is occupied by two large unpaired ossifications, an anterior one, the ethmosphenoid, and a posterior one, the otico-occipital. 5) The presence of two paired processes on the posterior part of the ethmosphenoid: a dorsal one, the processus antoticus (*pr. aot*, fig. 44; pl. 10, fig. 1)[1], and a ventral one, the processus basipterygoideus (*pr. bp*; cf. p. 386). The jugular vein passed backwards between these two processes, both of which were in articular connection with the palatoquadrate, the processus antoticus with the processus ascendens, the processus basipterygoideus with the processus basalis of the palatoquadrate. 6) The presence of a paired posteriorly projecting process, the processus connectens (*pr. conn*; *Porolepis*, pl. 3, fig. 2; pl. 4, figs. 1, 2; *Holoptychius*, fig. 44; *Eusthenopteron*, pl. 10; *Thursius*?, fig. 62 B; cf. Jarvik 1937, p. 73 and figs. 4, 5 A, B, 6, 8), at the posterior end of the ethmosphenoid. This process lies with its lateral side against the medial side of the antero-ventral corner of the part of the otico-occipital that constitutes the lateral wall of the fossa chordalis (fig. 62 B; cf. Romer 1937, figs. 2—4). 7) The very similar development of the otico-occipital (as regards *Osteolepiformes* see Säve-Söderbergh 1936, figs. 58, 59; Romer 1937, figs. 1—6; among *Porolepiformes* known in *Porolepis* only), including: a) The presence of a very wide fossa chordalis in the ventral median part of the otico-occipital bounded anteriorly by a pit in the posterior face of the ethmosphenoid (*fo. chd*, pl. 3, fig. 1; cf. Jarvik 1937, fig. 5 B, *p. sbc*), b) the position of the cranial cavity and labyrinth cavities in the otico-occipital, c) the general development and course of the main canals for nerves and vessels in the otico-occipital, d) the presence of a lateral ledge along the ventral part of the otico-occipital in front of the anterior orifice of the jugular canal, e) the presence of two articular areas for the hyomandibular situated dorsally and ventrally respectively to the posterior orifice of the jugular canal, f) the presence of a fossa Bridgei on the dorsal side of the otico-occipital above the otic capsule, and, finally, g) the fact that the occipital part of the otico-occipital is very short and high.

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[1] It may be pointed out in this connection that *Osteolepiformes* and *Porolepiformes* differ also in the development of the pectoral fin. The endoskeleton of the pectoral fin is of a dichotomical type in *Osteolepiformes* (*Eusthenopteron, Sauripterus*; HOLMGREN 1933, pp. 197—199, 288), as in *Anura*, whereas in *Porolepiformes* (*Holoptychius*) it is in all probability of an archipterygial type (cf. HOLMGREN 1933, p. 202), as in *Urodela*.

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[1] The processus antoticus in *Eusthenopteron* reminds in its general appearance of the basipterygoid process (*pr. bp*, pl. 10). It is badly crushed and damaged in the specimen shown in pl. 10, but was well preserved in the specimen used for grinding-series 2.

b. Comparison with other fishes.

Though mutually widely different as to the development of the nasal cavities the Elasmobranchs, Brachiopterygians, Actinopterygians and Dipnoans agree in that they are devoid of equivalents of the processus intermedius, the processus dermintermedius and the other formations by means of which the anterior and antero-lateral parts of the nasal cavity in *Osteolepiformes* are subdivided into compartments. The nasal cavity in the said four groups of fishes shows no indications whatever of any recesses corresponding to the recessus superior, recessus medius and recessus inferior in *Osteolepiformes.* Moreover these groups have no true choanae and no fossa apicalis. The n. profundus and r. palatinus VII are also developed differently in them to what must have been the case in *Osteolepiformes.*

A great many other differences are worthy of mention, but the few pointed out suffice to show that *Osteolepiformes* are widely different from Elasmobranchs, Brachiopterygians, Actinopterygians and Dipnoans as regards the development of the snout. It is quite evident both from the structure of the snout and from their organization otherwise that the *Osteolepiformes* cannot possibly be closely related to any of those four groups of fishes.

A comparison between *Osteolepiformes* and *Coelacanthiformes* will be given below after dealing with the latter group (pp. 593—597).

c. Comparison with Urodela.

In the development of the snout Urodeles agree fundamentally with *Porolepiformes* (pp. 417—421). The differences between Urodeles and *Osteolepiformes* with regard to the snout are thus essentially the same as those between *Porolepiformes* and *Osteolepiformes* (see pp. 488—494) and it is, therefore, superfluous to enter upon them here.

d. Comparison with Anura.

In a preceding chapter (pp. 392—424) I was able to demonstrate that as regards the structure of the snout *Porolepiformes* and *Urodela* show a great many points of agreement and it was concluded that the Urodeles must have arisen from *Porolepiformes* or in any case from Porolepiform-like ancestors. As we shall now see the *Osteolepiformes* are fundamentally as the *Anura* and it is quite evident that these two groups must be closely related and that the *Anura* must be derived from primitive *Osteolepiformes.*

Among the Anurans *Rana* was treated above in particular detail (pp. 308—333). In the subsequent account the *Osteolepiformes* will therefore above all be compared to that genus.

The internasal wall (*w. in*) is developed in much the same way in *Eusthenopteron* (figs. 51, 52 A, C, 57 A, B, 59, 70 A, 71 A; pp. 428, 439) and *Rana* (figs. 22, 27; p. 309). It does not house either any anterior (ethmoidal) part of the cranial cavity or any cavum internasale, but is a comparatively thin solid nasal septum (*sn*). Behind the nasal cavities it also extends backwards as a septum (*s. olf*, figs. 23 A, 24 A, 49, 50, 59, 65 A, 70 A) between the olfactory canals. This interolfactory septum is in *Eusthenopteron* continued backwards by a median ventral ridge (ri_v; p. 461) on the floor of the cranial cavity, which is not the case in *Rana*. In *Alytes* (Stadtmüller 1936, fig. 415 *k*; cf. also fig. 70 in the present work), on the other hand, there is a corresponding median ventral ridge, which, however, is but slightly developed. The olfactory canals and the septum (*s. olf*) between them extend much farther backwards in the interorbital wall in *Eusthenopteron* than in *Rana* and other Anurans (figs. 65, 70) and correlative with this the cranial cavity in *Eusthenopteron* does not go so far forwards as it does in Anurans. On the other hand, both the brain and the olfactory nerves in *Eusthenopteron* evidently had very much the same position and extent in relation to the interorbital wall and the ethmoidal region as they have in Anurans. While in *Eusthenopteron* (fig. 59) the foremost part of the cranial cavity was occupied by the brain, in Anurans it houses the hinder parts of the olfactory nerves situated behind the olfactory canals (figs. 24 B, 30). This part of the cranial cavity in Anurans thus has such a position within the interorbital wall and such relations to the brain and olfactory nerves that it must be regarded simply as a secondarily formed extension of the cranial cavity. A corresponding extension of the cranial cavity and a shortening of the olfactory canals would arise in *Eusthenopteron* if the hinder part of the septum (*s. olf*) between the olfactory canals disappeared and the space thus formed became somewhat widened through a reduction of the skeletal tissue nearest around it (see figs. 65, 70). Thus the differences between *Eusthenopteron* and Anurans as to the relative extent of the olfactory canals and the cranial cavity must be due to a more incomplete development of certain anterior internal parts of the interorbital wall in the latter forms.

Before entering upon the divisio prenasalis communis it is necessary to treat here certain of the dermal bones of the tip of the snout and the anterior part of the palate, viz. the naso-rostro-premaxillaries, the vomers and the parasphenoid.

In *Eusthenopteron* the premaxillary, medial rostral, and nasal 1 are usually fused into a naso-rostro-premaxillary (NRP, NRP_1, NRP_2, NRP_3, $pr_l NRP_3$, $pr_m NRP_3$, figs. 34, 56, 60, 64 A, 68 A, D, E, 72 A, 87 A; pl. 6, figs. 1, 2; pl. 7; pl. 8, fig. 1; pl. 9, fig. 1; pl. 10; pl. 11, figs. 1, 6; p. 347). This complex bone extends so far backwards as to enter into the boundary of the fenestra exochoanalis (*fe. exch*, fig. 56). The "premaxillary" in *Rana* (Pmx, Pmx_1, Pmx_2, Pmx_3, $pr_l Pmx_3$, $pr_m Pmx_3$, figs. 22 E, 23, 30, 31, 69; cf. figs. 64 B, 66, 68 B, C, 72 B, C; Ecker-Wiedersheim-Gaupp 1896, p. 52), on the other hand, ends much further anteriorly and does not reach the fenestra exochoanalis. In fact it has no equivalent to the part of the naso-rostro-premaxillary which in *Eusthenopteron* lies underneath the lateral rostral (*R. l*, fig. 68 A). That part is in *Rana* substituted by the maxillary, which goes much further forwards than in *Eusthenopteron* (cf. figs, 68 B, C). Both the pars facialis and the pars palatina of the lateral rostral must be assumed to be completely or almost completely reduced in Anurans (cf. p. 549), and it is very probable that also the absence of the underlying part of the "premaxillary" in Anurans is secondary and due to reduction. In connection with these reductions the maxillary in Anurans seems to have developed progressively in a forward direction to replace the reduced part of the "premaxillary". This is supported by the fact that the "premaxillary" in larvae of certain Anurans, e. g. *Pseudis* (W. K. Parker 1881, pl. 10, figs. 1, 3; pl. 12, figs. 2, 4), goes further backwards than in the adults, and judging from a figure published by Noble (1931, fig. 81 A; cf. De Villiers 1934, figs. 1—3) the "premaxillary" in *Ascaphus* (considered to be one of the most primitive Anurans) has a backward extent approximately similar to that of the naso-rostro-premaxillary in *Eusthenopteron*. The naso-rostro-premaxillary in *Eusthenopteron* consists morphologically of three parts, the pars dentalis (NRP_1), pars facialis (NRP_2) and pars palatina (NRP_3, figs. 56, 68 A, D, E, 72 A, 87 A), and is in this respect quite as the "premaxillary" in *Rana* (Pmx_1, Pmx_2, Pmx_3, figs. 23, 69; cf. fig. 72 B, C; Ecker-Wiedersheim-Gaupp 1896, p. 52). The partes faciales of the naso-rostro-premaxillaries in *Eusthenopteron* (NRP_2, figs. 68 A, D, E, 72 A; pl. 6, figs. 1, 2; pls. 7, 10) are more strongly developed than the similarly termed parts of the "premaxillaries" in the European *Rana* species, and contrary to conditions in these species they extend forwards to meet each other in a median suture. In certain non-European *Rana* species and in certain other Anurans, however, the pars facialis of the "premaxillary" is fairly strong and highly suggestive of the pars facialis of the naso-rostro-premaxillary in *Eusthenopteron*. Thus in *R. gracilis*, *R. hexadactyla*, *R. kuhli*, *Alytes* and others (W. K. Parker 1881, pl. 6, fig. 6; pl. 7, figs. 1, 6; pl. 24, fig. 1) the pars facialis is broad and suturates with its fellow in the median line. On the outside of its antero-dorso-medial corner there is a depressed area in these Anurans, which reminds of the area ($od.\,Ptr_a$, fig. 68 E) on the pars facialis of the naso-rostro-premaxillary in *Eusthenopteron* that is overlapped by the foremost median postrostral (Ptr_a, fig. 68 A). In *Pelodytes* (W. K. Parker 1881, pl. 23, fig. 1) the dorsal part of the pars facialis of the "premaxillary" is subdivided by a broad shallow emargination into two processes, one lateral and one medial. A corresponding subdivision of the dorsal margin of the naso-rostro-premaxillary into lateral and medial processes ($pr_l NRP_2$, $pr_m NRP_2$, fig. 68 D, E; cf. Westoll 1937 c, fig. 4) is often found in *Eusthenopteron*. The partes palatinae[1] in both forms (figs. 23 B, 87 A) have their antero-medial ends produced somewhat backwards, forming together a short median posterior process ($pr_m Pmx_3$, $pr_m NRP_3$), and each of them also has a lateral process ($pr_l Pmx_3$, $pr_l NRP_3$; cf. p. 450). In *Eusthenopteron* the lateral process is always suturally connected with the antero-lateral process (*pr. Vo*, figs. 56, 64 A; p. 451) of the vomer (*sut. Vo*, fig. 68 D), whereas in *Rana* it meets the vomer in certain specimens only (see p. 499).

From the above it is evident that the "premaxillary" in Anurans is a true homologue of the naso-rostro-premaxillary in *Eusthenopteron*. As the Anuran "premaxillary" must thus be regarded as a complex naso-rostro-premaxillary, as previously assumed by Säve-Söderbergh (1936, p. 156; figs. 62, 67), it might be expected to arise from three separate primordia during its embryonic development. As far as we know at present, this is not the case (Dugès 1835; W. K. Parker 1871; 1876; 1881; Hertwig 1874; Gaupp 1905; Erdmann 1933; Reinbach 1939). The embryonic development of the "premaxillary", however, proceeds very rapidly and its separate primordia may easily have been overlooked. It is of course also possible that owing to the rapid development of the bone the stage in which the primordia were separate is entirely suppressed.

The vomer (*Vo*) is developed in fundamentally the same way in *Eusthenopteron* (pp. 450—451; figs. 56, 64 A, 87 A) and *Rana* (figs. 23, 31; cf. fig. 64 B), formed in both of a horizontal plate and a descending tooth-bearing lamina (*la. Vo*). The descending tooth-bearing lamina is more complete, however, in *Eusthenopteron* than in *Rana*, where it lacks the posterior rostro-caudal portion and is separated from the corresponding lamina of the opposite side by a median interspace. Owing to this *Rana* lacks equivalents to both the intervomerine pit (*fo. iv*) and the intervomerine canal (*c. iv*) in *Eusthenopteron* (figs. 56, 58, 87 A; p. 459). It is interesting to note, however, that there are certain *Osteolepiformes* which in this respect are somewhat intermediate between *Eusthenopteron* and *Rana*, the tooth-bearing laminae of the vomers in them being more or less completely separated in the median line by a large foramen or interspace (fig. 62 B; p. 487). Both in *Eusthenopteron* and in *Rana* the horizontal plate of the vomer is produced into an antero-lateral process (*pr. Vo*), which, however, is much more strongly developed in the former than in the latter form. In *Eusthenopteron* a long part of this process is thus always in sutural connection with the lateral process ($pr_l NRP_3$) of the pars palatina of the naso-rostro-premaxillary (*sut. Vo*, fig. 68 D), whereas in *Rana* the process generally does not reach the corresponding process of the "premaxillary". However, it may sometimes also in *Rana* extend laterally so as to meet the said process of the "premaxillary" (Ecker-Wiedersheim-Gaupp 1896, fig. 14; Bhatia and Prashad 1918, fig. 2; Schaefer 1932, fig. 2). In certain other Anurans, e. g. *Calyptocephalus* (Reinbach 1939, pl. 16, fig. 8), it is normally so strongly developed that it has a long contact with the "premaxillary". When in Anurans the antero-lateral process of the vomer is in contact with the "premaxillary", it does not form any suture with that bone (as it does in *Eusthenopteron*) but simply overlaps its pars palatina. This is due to the fact that in Anurans the vomer is practically throughout situated higher in relation to the pars palatina of the "premaxillary" than in *Eusthenopteron*. If the Anurans are derived from primitive *Osteolepiformes*, it must be assumed that the vomer in them has secondarily acquired a more dorsal position in connection with a reduction of the ventral superficial parts of the ethmoidal region (cf. p. 508; No. 3, p. 509; No. 5, p. 510; cf. also figs. 71, 72). The medial part of the vomer is less complete in *Rana* than in *Eusthenopteron* and is devoid of an equivalent to the anteromedial corner that in *Eusthenopteron* forms the dorsal boundary of the intervomerine pit. The posterior process ($pr_p Vo$, fig. 64 A) of the vomer is absent in *Rana*, but is present in the primitive genus *Ascaphus* (De Villiers 1934, p. 16; cf. fig. 64 B), as it is in *Eusthenopteron*. Both in *Eusthenopteron* (figs. 56, 58, 64 A; p. 474) and in *Rana* (fig. 23 B; cf. figs. 31, 64 B) the vomer is pierced by the palatine canal (cf. p. 545). In both forms this canal enters the bone from the dorsal side and bifurcates into a medial and an antero-lateral branch ($c_m pal$, $c_{al} pal$), whose anterior orifices are situated on the lower side of the bone in front of the tooth-bearing lamina.

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[1] The pars palatina of the naso-rostro-premaxillary in *Eusthenopteron* is formed by the pars palatina of the premaxillary proper and dorsally to the antero-medial part of that by the palatal process (*R. m. pal*, fig. 56) of the medial rostral. The partes palatinae of the naso-rostro-premaxillaries thus constitute what has been described above (p. 450) as the palatal lamina (*la. pal*, fig. 58) of the ethmoidal shield, with the exception, however, of the palatal processes (*R. l. pal*) of the lateral rostrals.

The parasphenoid (*Psph*) in *Eusthenopteron* (figs. 50, 55, 56, 64 A, 87 A; pl. 8, fig. 1; pl. 12, figs. 3—6; pl. 13) is narrow like that in *Rana* (figs.

23, 24, 31; Ecker-Wiedersheim-Gaupp 1896, p. 50), but extends further forwards[1]. The reproductions given by Reinbach (1939, pl. 15, fig. 6; pl. 16, figs. 7, 8), however, show that in larvae of *Calyptocephalus* the parasphenoid extends approximately as far forwards as in *Eusthenopteron*, whereas in the adults it seems to have a somewhat smaller forward extent. The anterior part of the parasphenoid in *Calyptocephalus* thus probably undergoes a reduction at its anterior end in later larval stages. The parasphenoid in *Eusthenopteron* is provided with a ventral tooth-bearing ridge (*ri. Psph*), which has no equivalent in *Rana*.

In the foremost part of the palate there is both in *Eusthenopteron* (p. 429; figs. 56, 64 A, 87 A) and *Rana* (fig. 23 B) an anterior palatal fenestra (*fe. pal*), bounded anteriorly and antero-laterally by the partes palatinae of the naso-rostro-premaxillaries and the "premaxillaries" respectively, and posteriorly by the vomers. On account of the weaker development of the vomers this fenestra in *Rana* extends somewhat further backwards than the corresponding one in *Eusthenopteron*, though nevertheless it is situated mainly underneath the divisio prenasalis communis (cf. fig. 64 B). Accordingly the fenestra in question in *Eusthenopteron* is comparable only to the larger anterior part of that in *Rana*.

The anterior palatal fenestra in *Eusthenopteron* lies in the roof of a special fossa, the fossa apicalis (*fo. ap*, figs. 56, 64 A, 87 A; pp. 458—459), bounded anteriorly and laterally by the ventral parts of the naso-rostro-premaxillaries and posteriorly mainly by the transverse portions of the descending tooth-bearing laminae (*la. Vo*) of the vomers. A corresponding fossa is also distinguishable in *Rana* (see fig. 23 B; cf. also fig. 64 B), but owing to the weaker development of the tooth-bearing laminae the posterior boundary of this fossa is not at all so distinct as in *Eusthenopteron*.

In the anterior palatal fenestra in *Eusthenopteron* (figs. 56, 60, 64 A, 87 A) an area of the lower face of the divisio prenasalis communis is exposed. In either lateral end of this area is a depression

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[1] As is well known the parasphenoid in Crossopterygians does not extend further backwards than approximately to the transition between the orbitotemporal and otic regions, whereas in Anurans and the majority of Gnathostomes it goes much further backwards, in several forms even underneath the occipital region. In certain reptiles and birds (see De Beer 1937, pp. 233, 267, 280) the parasphenoid arises from two primordia, an anterior unpaired one situated underneath the orbitotemporal region, and a posterior paired one, and it is not impossible that this applies also to the parasphenoid in Amphibians (cf. Kruijtzer 1931, p. 145). According to Pehrson (1940, p. 38, fig. 39), it is very likely that also the parasphenoid in *Amia* arises in a similar manner. It is of great interest that in *Eusthenopteron* (grinding-series 2) we find a large paired tooth-bearing dermal plate underneath the otic region. These plates have such a position that they may very well correspond to the posterior part of the parasphenoid in reptiles and birds that arises from a paired primordium.

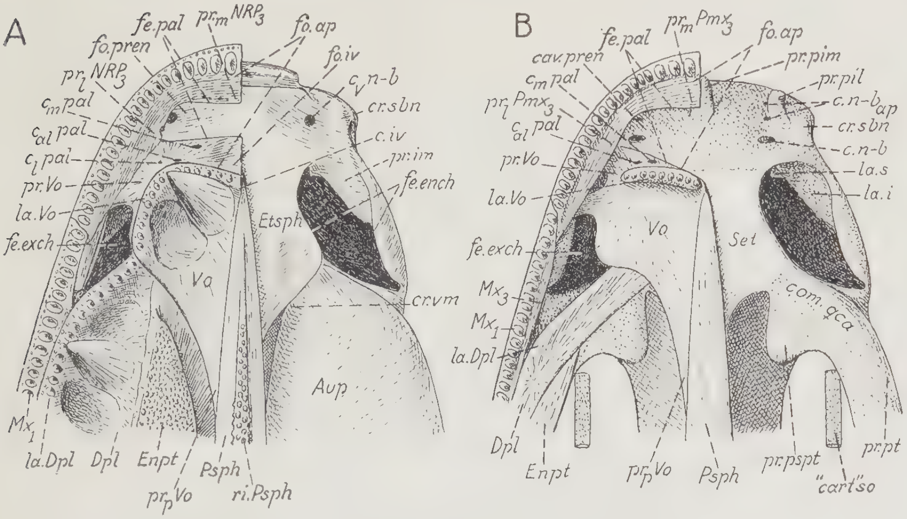
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Fig. 64. Two drawings illustrating probable transformations in the ventral parts of the snout during the development of Anurans from Osteolepiform Crossopterygian ancestors. The snout in ventral aspect. Dermal bones omitted on the left side. Cartilage dotted. *A*, *Eusthenopteron foordi* Whiteaves. $^2/_1$. *B*, hypothetic primitive Anuran.

Aup, pars autopalatina of palatoquadrate; *Dpl,* dermopalatine; *Enpt,* entopterygoid; *Etsph,* ethmosphenoid; Mx_1, Mx_3, pars dentalis and pars palatina of maxillary; *Psph,* parasphenoid; *Set,* sphenethmoid; *Vo,* vomer; $c_{al}pal$, canal for antero-lateral terminal branch of r. palatinus VII; *"cart"so,* "cartilago supraorbitalis", probably corresponding to the posterior independent part of the processus supraorbitalis lateralis in *Eusthenopteron foordi*; *cav. pren,* cavum prenasale, formed by widening of the prenasal pits in *Osteolepiformes*; *c. iv,* intervomerine canal; c_lpal, c_mpal, canals for lateral and medial terminal branches of r. palatinus VII; *c. n-b,* nasobasal canal; $c.\ n$-b_{ap}, apical part of nasobasal canal; *com. qca,* commissura quadrato-cranialis anterior; *cr. sbn,* crista subnasalis; *cr. vm,* ventro-medial crista of pars autopalatina; c_vn-b, ventral branch of nasobasal canal; *fe. ench,* fenestra endochoanalis; *fe. exch,* fenestra exochoanalis: *fe. pal,* anterior palatal fenestra; *fo. ap,* fossa apicalis; *fo. iv,* intervomerine pit; *fo. pren,* prenasal pit; *la. Dpl.* vertical lamina of dermopalatine; *la. i,* lamina inferior; *la. s,* lamina superior; *la. Vo,* descending tooth-bearing lamina of vomer; *pr. im,* processus intermedius of lamina nariochoanalis; pr_lNRP_3, pr_mNRP_3, lateral and medial processes of pars palatina of naso-rostro-premaxillary; pr_lPmx_3, pr_mPmx_3, lateral and medial processes of pars palatina of Anuran "premaxillary", homologous to the correspondingly situated processes of naso-rostro-premaxillary in *Osteolepiformes*; *pr. pil,* processus prenasalis inferior lateralis; *pr. pim,* processus prenasalis inferior medius; *pr. pspt,* processus pseudopterygoideus; *pr. pt,* palatoquadrate bar ("processus pterygoideus"); pr_pVo, posterior process of vomer; *pr. Vo,* antero-lateral process of vomer; *ri. Psph,* ventral tooth-bearing ridge of parasphenoid.

which constitutes the anterior part of the prenasal pit (*fo. pren*; p. 459). A close comparison shows that the anterior parts of the prenasal pits in *Eusthenopteron* have such topographic relations to the skeleton and nerves that they must correspond to the cavum prenasale in *Rana* (p. 309; *cav. pren*, figs. 22 A, 23 B; cf. figs. 64 B, 72 C). They are situated dorsally to the level of the anterior palatal fenestra and open ventrally through that fenestra, just as the cavum prenasale in

Rana. The divisio prenasalis communis in *Eusthenopteron* is covered anteriorly and antero-laterally on either side by the partes faciales of the naso-rostro-premaxillaries and ventrally in front of the anterior palatal fenestra by the partes palatinae; in *Rana* the corresponding parts of the "premaxillaries" form the anterior and antero-lateral and in front of the anterior palatal fenestra the ventral boundaries of the cavum prenasale. The lateral part of the divisio prenasalis communis in *Eusthenopteron* forms a thick prenasal wall on either side, whose ventral medial portion is pierced in a rostro-caudal direction by the nasobasal canal (*c. n-b*, figs. 52, 57) for the r. medialis narium of the n. profundus (p. 476; *r. mn*, figs. 59, 61). In *Rana* the cavum prenasale is bounded posteriorly on either side by the thin prenasal wall, whose ventral medial part is perforated by the fenestra nasobasalis (p. 311; *fe. nb*, fig. 22 B, C; cf. fig. 22 E and *fe. n-b*, fig. 72 B, C) through which emerges the r. medialis narium of the n. profundus (p. 328; *r. mn*, figs. 29, 30). The nasobasal canal in *Eusthenopteron* gives off a ventral branch ($c_{v}n\text{-}b$, figs. 56, 57 B—D, 64 A) leading down to the anterior part of the prenasal pit and then bifurcates into two anterior branches ($c_{m}n\text{-}b$, $c_{l}n\text{-}b$), almost horizontal and slightly diverging forwards, their anterior orifices being on the anterior face of the prenasal wall (fig. 47 C). These three canal branches transmitted nerve branches ($r_{v}mn$, $r_{m}ap$, $r_{l}ap$, figs. 59—61; pp. 476—477) homologous to the ventral, medial and lateral terminal branches of the r. medialis narium of the n. profundus in *Rana* (see p. 542). The ventral terminal branch ($r_{v}mn$) in *Eusthenopteron* emerged in the lateral part of the prenasal pit and then as in *Rana* traversed the lateral part of the anterior palatal fenestra and probably formed a prenasal anastomosis (pp. 329, 477, 480; *ast. pren*, figs. 29, 31, 60, 61) with the medial terminal branch of the r. palatinus VII. After giving off this ventral branch the r. medialis narium in *Rana* bifurcates into its medial and lateral terminal branches ($r_{m}ap$, $r_{l}ap$, fig. 30) both of which go almost straight forwards through the medial parts of the cavum prenasale. In *Eusthenopteron* the corresponding branches (figs. 59, 61) traversed the anterior branches ($c_{m}n\text{-}b$, $c_{l}n\text{-}b$) of the nasobasal canal and thus had a very similar course. The terminal branches of the r. medialis narium in *Eusthenopteron* thus ran almost exactly as do the corresponding ones in *Rana*, with the difference, however, that they are to a large extent enclosed in the prenasal wall whereas in *Rana* they traverse the cavum prenasale. — It is thus obvious that the anterior parts of the prenasal pits in *Eusthenopteron* may in fact be regarded as a cavum prenasale in an initial stage of development. If they were widened by a reduction of the anterior parts of the divisio prenasalis communis so that there remained only certain anterior parts of the endoskeleton necessary for the support of the naso-rostro-premaxillaries (see pp. 504—505), a space would obviously arise which in all essentials would agree with the cavum prenasale in *Rana* (see figs. 64, 67, 70, 72). Like that it would be bounded anteriorly and ventrally by the partes faciales and partes palatinae of the "premaxillaries" and posteriorly on either side by the fairly thin prenasal wall and it would be traversed by the terminal branches of the r. medialis narium. The fenestra nasobasalis in *Rana*, which sometimes (ECKER-WIEDERSHEIM-GAUPP 1896, fig. 16) as is normally the case in several other Anurans (fig. 22 E), may be a comparatively small opening, thus represents a remainder of the nasobasal canal in *Eusthenopteron*. More precisely it represents the part of the nasobasal canal in *Eusthenopteron* that lies about midway between the posterior orifice and the place where the ventral canal branch ($c_v n\text{-}b$, fig. 57 B, C) is given off. The posterior part of the nasobasal canal is absent in consequence of reductions in the posterior parts of the prenasal wall which must have taken place within the Anurans (see pp. 527—535), whereas the anterior part of the nasobasal canal has become reduced by the development of the cavum prenasale. It is interesting to find that in larval stages of *Calyptocephalus* there persists, in front of the fenestra nasobasalis, a part of the nasobasal canal traversed by the medial and lateral terminal branches (cf. $r_m ap$, $r_l ap$, fig. 30) of the r. medialis narium (REINBACH 1939, pp. 257—258, 261; cf. fig. 64 B, $c.\,n\text{-}b_{ap}$). It is also noticeable that the fenestra nasobasalis in *Calyptocephalus* is comparatively small in early larval stages, but increases in width later on during the larval development (REINBACH 1939, p. 264; "fenestra apicalis").

The hinder part of the prenasal pit (*fo.pren*, figs. 56, 58 A, 64 A) in *Eusthenopteron* is situated in the thin antero-lateral part of the vomer. If the ventral parts of the ethmoidal region in *Eusthenopteron* were reduced in the way shown in fig. 70 (cf. figs. 64, 72) and in connection with this reduction the vomer shifted upwards to gain support against the endocranium, the prenasal pits would be extended backwards and medially so as to fuse postero-medially with each other. If then the antero-medial parts of the vomers were also reduced, a space would obviously arise essentially corresponding to the cavum subnasale in *Rana* (p. 309; *cav. sbn*, fig. 23 B; cf. fig. 72 C). If the nasal cavities widened forwards at the cost of the posterior part of the prenasal wall, as they must be assumed to have done in Anurans (cf. pp. 534—535), the space in question would be situated mainly underneath the anterior parts of the septum nasi and underneath the anterior parts of the nasal capsules, i. e. as in *Rana*.

The prenasal pits in *Eusthenopteron* are separated from each other by a broad median rostro-caudal ridge (figs. 48, 64 A). It is not unlikely that the median unpaired processus prenasalis inferior medius (Gaupp 1905, p. 733; Stadtmüller 1936, p. 562) which occurs in several Anurans (*Rana tigrina*, *Rappia*, *Hyla* and others; Bhatia and Prashad 1918, p. 7; fig. 7; W. K. Parker 1881, pl. 6, figs. 1, 2; pl. 28, figs. 6, 7; pl. 32, figs. 2, 4) may be a vestige of that ridge in *Eusthenopteron* (*pr.pim*, figs. 64 B, 67 B). This may possibly apply also to the isolated median cartilage in *Bufo* (Schoonees 1930, pp. 461—462, figs. 7, 8; *m.p.K*) which lies between the partes palatinae of the "premaxillaries".

The ventro-lateral corner of the prenasal wall in *Eusthenopteron* (*w.a*, figs. 47 A, B, 57 B, 59) is provided with a distinct ventral crest, the crista subnasalis (*cr.sbn*, figs. 47 B, C, 48, 64 A, 67 A, 71 A), situated laterally to the prenasal pit and to the ventral branch ($c_vn\text{-}b$) of the naso-basal canal which transmitted the ventral terminal branch (r_vmn) of the r. medialis narium of n. profundus. Against the lower and medial side of this crest rest the foremost part of the lateral process (pr_lNRP_3, figs. 56, 64 A, 68 D) of the pars palatina of the naso-rostro-premaxillary and the ridge $ri.NRP_3$ (fig. 68 D; p. 434) on the dorsal face of this process. The corresponding lateral process of the pars palatina of the "premaxillary" in *Rana* (pr_lPmx_3, fig. 23 B; p. 498) also lies with its external face against the medial face of a crista subnasalis (*cr.sbn*, fig. 22 A, B; cf. figs. 22 E, 64 B, 67 B, C, 71 B, C). This crest in *Rana* forms a ventrally projecting elevation of the ventro-lateral corner of the prenasal wall laterally to that part of the cavum prenasale in which the ventral terminal branch (r_vmn) of the r. medialis narium bends downwards. It is thus evident that the crista subnasalis in *Eusthenopteron* agrees so completely with the crista subnasalis in *Rana* that they may be regarded as homologous formations (cf. figs. 64, 67, 71).

Besides by the crista subnasalis the "premaxillary" in *Rana* is supported by two anteriorly directed prenasal endoskeletal processes (p. 309; figs. 22 A—C, 23 B, 31; cf. figs. 64 B, 67 B, C, 70 B, C, 72 B, C), an upper, processus prenasalis superior lateralis (*pr.psl*), and a lower, processus prenasalis inferior lateralis (*pr.pil*). These two endoskeletal processes fit into special pits on the hinder face of the pars facialis of the "premaxillary" (Pmx_2). The upper one of these pits lies near the dorsal margin of the pars facialis, whereas the lower pit is situated close above the pars palatina. The posterior (internal) face of the pars facialis of the naso-rostro-premaxillary in *Eusthenopteron* is divided into two divisions, one lateral and one medial, by the foremost and almost vertical part of the supraorbital sensory canal ridge (*ri.soc*, fig. 68 D) which occupies the foremost part of the groove *gr.soc* (fig. 47) on the dorsal face of the ethmoidal region. Two groups of small foramina ($f.ap_l$, $f.ap_m$, fig. 68 D) on the posterior face of the facial part of the naso-rostro-premaxillary show that the apical twigs (*rr. ap*, figs. 59—61) of the lateral and medial terminal branches (r_lap, r_map) of the r. medialis narium entered the pars facialis partly close below, partly close medially to the supraorbital sensory canal ridge (*ri. soc*). In the European *Rana* the lateral and medial terminal branches (r_lap, r_map, fig. 30) of the r. medialis narium pass forward medially to the ventral part of the pars facialis of the "premaxillary" and break up into their apical twigs just in front of the "premaxillary". It is thus obvious that the entire pars facialis in the European *Rana* (cf. p. 497) represents only the lateral division of the pars facialis of the naso-rostro-premaxillary in *Eusthenopteron*, that is to say the division situated laterally to the supraorbital sensory canal ridge (*ri. soc*). Accordingly the homologues of the two endoskeletal prenasal processes in *Rana* must be sought for in *Eusthenopteron* in the antero-lateral portion of the divisio prenasalis communis that lies laterally to the groove *gr. soc* and is covered by the lateral division of the pars facialis of the naso-rostro-premaxillary. The lateral part of the pars facialis in *Eusthenopteron* is produced upwards into a more or less pronounced dorsal process (pr_lNRP_2, fig. 68 D, E; cf. p. 498) which is wedged in between the anterior tectal (*Te. a*, figs. 34, 68 A) laterally and the foremost normally independent nasal element (Na_2) dorso-medially. This process covers the part of the divisio prenasalis communis that forms the middle dorsal portion of the prenasal wall (figs. 34, 68 A). If in a form like *Eusthenopteron* the endoskeleton were to disappear all around a small remaining antero-dorso-lateral portion of the divisio prenasalis communis necessary for the support of the dorsal end of the pars facialis of the naso-rostro-premaxillary there would result a process suggestive of the processus prenasalis superior lateralis in *Rana* (*pr. psl*, figs. 67, 70, 72). — The lower prenasal process in *Rana* (*pr. pil*) projects from the solum nasi postero-laterally to the fenestra nasobasalis. A corresponding process may easily be imagined to develop from the part of the divisio prenasalis communis in *Eusthenopteron* that is situated immediately laterally to the anterior part of the canalis nasobasalis and the lateral terminal branch of that canal (figs. 64, 67, 70—72).

The prenasal and subnasal cavities in *Rana* house the intermaxillary gland (p. 322). Several conditions, such as the presence of the paired prenasal pit, which, as we have seen, represents the prenasal and subnasal cavities in *Rana* in an initial stage of development, the presence of the intervomerine pit, and the presence of the median intervomerine canal leading backwards from the fossa apicalis to the main posterior part of the mouth cavity, indicate that the fossa apicalis in *Eusthenopteron* probably lodged an intermaxillary gland homologous to that in

Anurans (cf. Jarvik 1937, p. 118). This presumed intermaxillary gland in *Eusthenopteron* was probably small and may have occupied mainly the prenasal pits — not the intervomerine pit, as previously maintained by the present writer (Jarvik 1937, loc. cit.) — and if so it was probably either paired or subdivided into two portions. This is of interest, for the intermaxillary gland arises in *Bufo* from a paired primordium and is said to be paired in adults of *Xenopus* (p. 322). The intermaxillary gland in Anurans has several efferent ducts running posteriorly (*gl. imxd*, fig. 31) and it is thus likely that this was the case also in *Eusthenopteron*. The efferent ducts of the intermaxillary gland in *Eusthenopteron* probably converged backwards towards the intervomerine pit to unite there into a common efferent duct passing backwards through the intervomerine canal and opening with an unpaired median orifice underneath the foremost part of the parasphenoid. It would thus appear as if the efferent ducts of the presumed intermaxillary gland in *Eusthenopteron* most closely resembled those in the Anuran genus *Arthroleptides* (p. 322).

In *Rana* and other Anurans tubes of the intermaxillary gland penetrate into the nasal cavity through the fenestra nasobasalis. It is not quite out of question that also in *Eusthenopteron* a few tubes of the intermaxillary gland extended dorsally and backwards into the nasal cavity through the ventral branch (c_v-*n-b*) and the posterior unbranched part of the nasobasal canal (*c. n-b*, fig. 57), both of which are comparatively wide, certainly much wider than the nerves and vessels which passed through them (see fig. 59).

The intermaxillary gland in *Eusthenopteron*, situated mainly in and just underneath the shallow prenasal pits, must have been fairly small. The intermaxillary gland in Anurans, on the other hand, is large and fills up both the subnasal and prenasal cavities, extending in the latter upwards to close below the skin of the dorsal side of the snout. As the small intermaxillary gland in *Eusthenopteron* undoubtedly represents a primitive condition, it follows that the intermaxillary gland in Anurans must have undergone a progressive development. Its increase in size obviously took place in connection with a reduction of certain parts of the divisio prenasalis communis, causing an excessive development of prenasal pits similar to those in *Eusthenopteron* into the subnasal and prenasal cavities in Anurans. Possibly this reduction was directly caused by the increase in size of the intermaxillary gland; a similar opinion has been advanced by several previous writers (see Stadtmüller 1936, pp. 561—562). From what is known concerning the Anurans it is evident, however, that their snout has undergone a general reduction both of the endoskeleton and the exoskeleton. This general reduction may

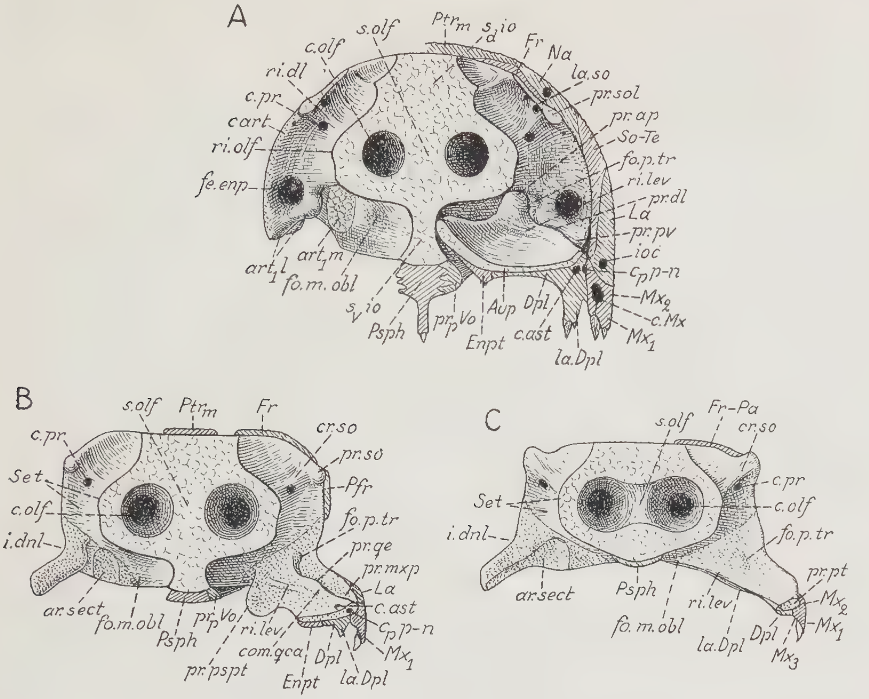
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Fig. 65. Three drawings illustrating probable transformations in the posterior parts of the snout during the evolution of Anurans from Osteolepiform Crossopterygian ancestors. The snout shown in posterior view. The palatoquadrate and the dermal bones omitted on the left side. The interorbital wall cut off close behind the ethmoidal region. Section areas through cartilage-bone reticulated, cartilage dotted. *A*, *Eusthenopteron foordi* Whiteaves. $^2/_1$. *B*, *C*, two hypothetic primitive Anuran forms, a very primitive one (*B*) and a somewhat more advanced one (*C*). The fusion of the commissura quadrato-cranialis anterior with the postnasal wall considered to have taken place as maintained by REINBACH (1939).

Aup, pars autopalatina of palatoquadrate; *Dpl*, dermopalatine; *Enpt*, entopterygoid; *Fr*, frontal; *Fr-Pa*, fronto-parietal; *La*, lachrymal; Mx_1, Mx_2, Mx_3, pars dentalis, pars facialis and pars palatina of maxillary; *Na*, nasal; *Pfr*, Anuran prefrontal, probably homologous to the supraorbito-tectal in *Osteolepiformes*; *Psph*, parasphenoid; Ptr_m, posterior median postrostral; *Set*, sphenethmoid; *So-Te*, supraorbito-tectal; *ar. sect*, section area through palatoquadrate; art_1l, art_1m, lateral and medial autopalatine articular areas; *cart*, superficial cartilaginous part of endocranium; *c. ast*, canal for postchoanal nerve anastomosis; *c. Mx*, canal for nerve to maxillary teeth; *c. olf*, canalis olfactorius; *com. qca*, commissura quadrato-cranialis anterior; $c_pp\text{-}n$, posterior palatonasal canal; *c. pr*, profundus canal; *cr. so*, crista supraorbitalis, probably homologous to the dorso-lateral ridge (*ri. dl*) of the postnasal wall in *Osteolepiformes*; *fe. enp*, fenestra endonarina posterior; *fo. m. obl*, pit for origin of oblique eye muscles (in *B* and *C* only for origin of m. obliquus superior); *fo. p. tr*, pit or area for insertion of portio transversalis of m. levator bulbi; *i. dnl*, notch in lateral margin of the postnasal wall in *Anura*, developed for the ductus nasolacrimalis and corresponding to the fenestra endonarina posterior in *Osteolepiformes*; *ioc*, infraorbital sensory canal; *la. Dpl*, vertical lamina of dermopalatine; *la. so*, lamina supraorbitalis; *pr. ap*, processus apicalis of pars autopalatina; *pr. dl*, dorso-lateral process of pars autopalatina; *pr. mxp*, processus maxillaris posterior of larval Anurans, probably homologous to the process *pr. pv* in *Osteolepiformes*; *pr. pspt*, processus pseudopterygoideus; *pr. pt*, palatoquadrate bar ("processus pterygoideus"); *pr. pv*, postero-ventral process of ethmoidal region; pr_pVo, posterior process of vomer; *pr. qe*, processus quadrato-ethmoivery well also have played a part in the development of the subnasal and prenasal cavities.

The postnasal wall and the anterior parts of the interorbital wall in *Eusthenopteron* (figs. 47 B, 49—51, 65 A, 67 A) both possess several characters making it difficult to compare them to the corresponding parts of the endocranium in *Rana* (figs. 22 A, D, 23 A). In accordance with the general shape of the endocranium the postnasal and interorbital walls are narrower and higher in *Eusthenopteron* and different also in their other proportions. Moreover, the postnasal and interorbital walls are more completely developed in *Eusthenopteron* than in *Rana*. Finally, the fact that the palatoquadrate is not fused with the endocranium in *Eusthenopteron* in the same way as it is in the adult *Rana* causes several special differences in the development of the lower parts of the postnasal wall (cf. pp. 520—525).

Evidently the differences between *Eusthenopteron* and *Rana* as regards the postnasal and interorbital walls are chiefly due to secondary modifications in the latter form. The endocranial parts in the posterior portion of the snout of Anurans may be assumed to have developed from conditions like those in *Osteolepiformes* in about the following way (figs. 65, 67). 1) The snout became lower and broader. This implied certain reductions and caused the thin dorsal and ventral parts of the interorbital wall ($s_{d}io$, $s_{v}io$) and the adjacent dorsal and ventral parts of the ethmoidal region to disappear. The uppermost part of the posterior face of the postnasal wall bearing the dorso-medial and dorso-lateral pits and the dorso-medial ridge separating these pits (*fo. dm*, *fo. dl*, *ri. dm*, figs. 49, 50) disappeared completely, but the dorso-lateral ridge (*ri. dl*) persisted (cf. p. 511). The posterior orifice of the profundus canal (*c. pr*), though retaining its position close ventrally to the dorso-lateral ridge (*ri. dl*), thus became situated in the dorso-medial corner of the posterior face of the postnasal wall (figs. 22 A, 23, 65 B, C, 66) instead of somewhat above the middle of the face as in *Eusthenopteron* (figs. 49, 50, 65 A). The roof and floor of the foremost parts of the cranial cavity became comparatively thin and the "basal angle" ("*ba*", fig. 47 B; foot-note 1, p. 432) disappeared. After these modifications the foremost part of the interorbital wall would in transverse sections be of a shape somewhat as shown in fig. 65 B and C. 2) Owing to the reductions

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dalis of larval Anurans, corresponding to the process *pr. dl* in *Osteolepiformes*; *pr. so*, processus supraorbitalis of *Rappia*, probably homologous to the lateral thickened part of the supraorbital lamina in *Osteolepiformes*; *pr. sol*, processus supraorbitalis lateralis; *ri. dl*, dorso-lateral ridge of postnasal wall; *ri. lev*, ridge or area for origin of principal portion of m. levator bulbi; *ri. olf*, olfactory ridge; $s_{d}io$, thin dorsal part of interorbital wall; *s. olf*, median septum between canales olfactorii; $s_{v}io$, thin ventral part of interorbital wall.

of the endoskeleton on the lower side of the ethmoidal region the parasphenoid and vomer shifted upwards, so that the latter bone became situated at a higher level than the pars palatina of the "premaxillary". 3) Through a reduction of certain internal anterior parts of the interorbital wall around the hinder parts of the olfactory nerves an anterior precerebral space developed, which was added to the cranial cavity (see p. 496). The palatoquadrate fused with the ventral lateral parts of the postnasal wall. — On the whole, modifications like those here outlined would lead to the development of a snout with the postnasal wall and the foremost part of the interorbital wall much as in *Rana cyanophlyctis* (fig. 24 A) and *Bufo* (fig. 66).

Both above and in other connections it has been mentioned that considerable reductions must have taken place in the endoskeleton of the snout in Anurans. That this actually is so and that the posterior part of the snout in Anurans must have undergone changes in shape somewhat similar to those just outlined is borne out by the following facts.

1) The posterior part of the ethmoidal region in *Rana* does not assume its characteristic broad and low shape until late during the larval development (Gaupp 1893, p. 424; pl. 15, fig. 30; cf. fig. 23 A of an adult *Rana* in the present work). A corresponding change in the proportions of the posterior parts of the ethmoidal region is known to take place also in the larval development of other Anurans, e. g. *Calyptocephalus* (Reinbach 1939, p. 264).

2) In certain *Rana* species (*R. cyanophlyctis*, fig. 24 A) there is a fairly high and narrow dorsal part ($s_d io$) of the interorbital wall above the olfactory canals (cf. figs. 23 A, 66). Also the part of the interorbital wall ($s_v io$, fig. 24 A) situated below the olfactory canals is comparatively high.

3) The vomer (*Vo*) and parasphenoid (*Psph*) in Anurans are situated on a level somewhat above that of the partes palatinae of the "premaxillaries" (Pmx_3, $pr_l Pmx_3$, figs. 22 E, 23, 64 B, 66) and maxillaries (Mx_3, fig. 27).

4) In *R. cyanophlyctis* (fig. 24 A) there is a small rod-like cartilage underneath the interorbital wall between that and the parasphenoid (Ramaswami 1935, p. 12; 1939, p. 50). This cartilage, which has incorrectly been termed the subethmoidal cartilage (see No. 5 below), is probably a remainder of the lowermost part of the interorbital wall in *Osteolepiformes*. A support for this opinion is found in the conditions in *Eusthenopteron*. In certain specimens of this form (gr.-ser. 2; pl. 13, figs. 4, 5) the thin ventral part ($s_v io$) of the interorbital wall shows an irregular fenestra. As its margins are not lined with periostal bone, this fenestra was probably closed by cartilage. Its ventral boundary consists of a narrow bridge of bone which is partly enclosed in the

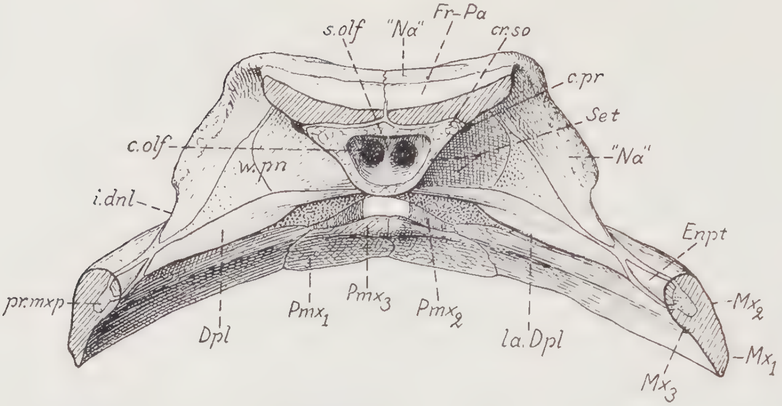

Fig. 66. *Bufo marinus.* Skeleton of snout in posterior view. After a specimen from Columbia, belonging to the Palaeozoological Department of the Swedish Museum of Natural History. Cartilage dotted. Cross-sections through cartilage-bone reticulated. $^3/_1$.

Dpl, dermopalatine; *Enpt,* entopterygoid; *Fr-Pa,* fronto-parietal; Mx_1, Mx_2, Mx_3, pars dentalis, pars facialis and pars palatina of maxillary; "*Na*", "nasal"; Pmx_1, Pmx_2, Pmx_3, pars dentalis, pars facialis and pars palatina of "premaxillary"; *Set,* sphenethmoid; *c. olf,* canalis olfactorius; *c. pr,* profundus canal; *cr. so,* crista supraorbitalis; *i. dnl,* notch for ductus nasolacrimalis; *la. Dpl,* vertical lamina of dermopalatine; *pr. mxp,* palatoquadrate bar, according to REINBACH's interpretation; processus maxillaris posterior of postnasal wall, according to GAUPP and PUSEY; *s. olf,* median septum between the olfactory canals; *w. pn,* postnasal wall.

parasphenoid and thus has fundamentally the same position as the "subethmoidal cartilage" in *Rana cyanophlyctis.*

5) In *Rana grayi* (C. A. DU TOIT 1933, pp. 724—725; fig. 3) there is an independent unpaired thin and broad cartilaginous plate, the subethmoidal cartilage, underneath the median parts of the ethmoidal region and thus further forwards than the "subethmoidal cartilage" in *R. cyanophlyctis.* Judging from its position this plate may very well represent a remainder of the ventral median parts of the ethmoidal region in *Osteolepiformes.*

6) In *Eusthenopteron* there are certain unossified parts in the interorbital wall (the fenestra referred to above under 4) and in the posterior dorso-lateral parts of the ethmoidal region (p. 427; *cart,* fig. 47), which indicates that a regressive development of the endoskeleton of the snout had already to some slight extent commenced in the *Osteolepiformes.*

The postnasal wall in both *Eusthenopteron* and *Rana* is pierced by a single profundus canal (*c.pr,* figs. 22 A, D, 23, 30, 49—51, 57, 59, 65 A; cf. fig. 66). In both forms this canal leads forwards to the posterior dorsal part of the nasal cavity close dorso-laterally to the olfactory canal (*c.olf,* figs. 22 D, 51). It is fairly short and not particularly wide (cf. *Porolepiformes* and Urodeles, pp. 291, 273; *f. prm,* fig. 16 C; *c. prm,* figs. 36 B, 37 B, 42). During its passage through the postnasal wall it sometimes bifurcates into two branches, medial and lateral (pp. 315, 470; *c. ln*, *c. mn*, figs. 51, 57 A, C, E), which open through separate orifices in the nasal cavity.

The posterior orifice of the profundus canal in *Eusthenopteron* lies close below the dorso-lateral ridge (*ri. dl*, figs. 49, 50, 65 A; p. 436), which extends from laterally and above in a direction medially downwards and continues backwards onto the foremost part of the lateral face of the interorbital wall. In Anurans there is a similarly situated ridge, the crista supraorbitalis (*cr. so*, figs. 22 A, 23 A, 24, 66; p. 315; cf. figs. 65 B, C, 67 C), at the antero-dorso-medial corner of the orbit and close above the profundus foramen. This ridge is described by Reinbach (1939, pp. 255—256) in the following way in *Calyptocephalus*: "Der Winkel, den das Planum antorbitale mit der Schädelseitenwand der Regio orbitotemporalis bildet, ist ausgerundet; im oberen Teil dieses Winkels geht vom Planum eine kurze, aber hohe und besonders dorsal sehr dicke Leiste aus, die an ihrem unteren Rand mit der Schädelseitenwand zusammenhängt". This ridge in Anurans is probably a homologue of the dorso-lateral ridge (*ri. dl*) in *Eusthenopteron*. Its somewhat different position is certainly due to the secondary modifications of the postnasal wall in Anurans (see above and figs. 65, 67).

Laterally to the dorso-lateral end of the dorso-lateral ridge (*ri. dl*) in *Eusthenopteron*, which thus presumably is the homologue of the crista supraorbitalis in Anurans, we find the thickened ventro-lateral part of the lamina supraorbitalis (*la. so*, fig. 65 A), which is produced backwards, forming the processus supraorbitalis lateralis (*pr. sol*, fig. 67 A). The hindmost part of this process in *Eusthenopteron foordi* constitutes an independent skeletal element or at least an independent ossification (p. 436). Laterally to the upper end of the crista supraorbitalis certain Anuran forms (*Rappia*, p. 317) have a small posterior process on the postnasal wall. Behind the upper margin of the postnasal wall certain other Anurans (*Alytes*, *Hyla* and *Phyllomedusa*; p. 317) have a small isolated cartilage, the "cartilago supraorbitalis". The posterior process and the isolated cartilage in Anurans just referred to are thus situated very much as the thickened ventro-lateral part of the lamina supraorbitalis and the isolated posterior part of the processus supraorbitalis lateralis, respectively, in *Eusthenopteron* (see figs. 65 B, 67 B, *pr. so*, *"cart" so*), and it is therefore possible that they correspond to them.

The pit *fo. m. obl* in *Eusthenopteron* (figs. 48—50, 55, 65 A) lies in the ventral part of the antero-medial corner of the orbit just above a shallow notch (*i. obl*) in the dorso-medial margin of the adjacent part of the pars autopalatina of the palatoquadrate. It has already been pointed out (pp. 437, 456) that this pit probably was the place of origin of the oblique muscles of the eye, and this is corroborated by the conditions in *Rana*. In the latter form the m. obliquus superior (*m. obl. s*, fig. 29) originates from the ventral part of the angle between the postnasal and interorbital walls just above and behind the m. obliquus inferior (*m. obl. i*, figs. 29, 31), which takes its origin from the adjacent medial end of the dermopalatine. The dermopalatine in *Eusthenopteron* lies fundamentally as in *Rana*, but is separated from the orbit by the strongly developed pars autopalatina of the palatoquadrate (cf. figs. 64, 65, 70). In these circumstances it must be concluded that both the m. obliquus superior and the m. obliquus inferior in *Eusthenopteron* originated in the pit *fo. m. obl.* In Anurans the origin of the m. obliquus inferior has obviously shifted downwards to the dermopalatine in connection with the changes in the development and connections of the palatoquadrate (pp. 520—525).

The ventro-lateral part of the postnasal wall in *Eusthenopteron* is pierced by a fairly wide foramen, the fenestra endonarina posterior (*fe. enp*, figs. 49—51, 65 A; pp. 446—447), which connects the posterior part of the nasal cavity with the orbit. No foramen of this kind is present in Anurans, but in them we find instead a more or less distinct incisure (*i. dnl*, figs. 65 B, C, 67 B, C) at almost the same place in the lateral margin of the postnasal wall (cf. SCHOONEES 1930, fig. 4; DE VILLIERS 1931 c, fig. 2; C. A. DU TOIT 1933; D. S. WAGNER 1934, fig. 3; STADTMÜLLER 1936, fig. 415 *k*)[1]. In this incisure, which is indistinct in *Rana* (figs. 22 D, 23 A), lies the nasolachrymal duct (*dnl*, figs. 29, 30) and the nerves and vessels passing along that duct. The part of the postnasal wall situated below the incisure is low and forms but a narrow skeletal bar connecting the other parts of the postnasal wall with the pars triangularis (p. 315; *p. tri*, fig. 22 A, D; the incisure hardly discernible in this figure). Ventrally to this low bar-like part of the postnasal wall and medially to the pars triangularis, which is curved slightly medially, lies the hindmost part of the sinus lateralis nasi (*sin. l*, figs. 27 A, 28 B; p. 325) and the adjacent foremost part of the sulcus maxillo-palatinus (*sulc. mx-pal*, fig. 27 B). If we imagine that in *Eusthenopteron* the lateral boundary of the fenestra endonarina posterior (presumably partly cartilaginous, *cart*, figs. 65 A, 67 A) was reduced (cf. figs. 65, 67), this fenestra would be transformed into an incisure in the lateral margin of the postnasal wall, resembling the incisure (*i. dnl*) for the nasolachrymal duct in Anurans. The ventral wall of the fenestra endonarina posterior in *Eusthenopteron* would then be a low skeletal bar protruding ventro-laterally and would thus be exactly like the low ventral part of the postnasal wall in Anurans that lies ventrally to the incisure (*i. dnl*) for the nasolachrymal duct. Ventrally to that skeletal bar and medially to the adjacent part of the lateral nasal wall (*w. lic*) that is curved medially, *Eusthenopteron* (p. 536) probably possessed structures homologous to the sinus lateralis nasi and the sulcus maxillo-palatinus in Anurans. Conditions in Anurans thus strongly support the above interpretation (pp. 446—447) that the wide foramen (*fe. enp*) in the ventrolateral part of the postnasal wall in *Eusthenopteron* is a true fenestra endonarina posterior, which gave passage to a posterior external nasal tube developed as a nasolachrymal duct.

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[1] In such forms as *Bufo*, where the "nasal" ("*Na*", fig. 66) is strongly developed and covers the lateral side of the postnasal wall, this incisure (*i. dnl*) is developed in the ventral part of the lateral margin of that bone.

The lateral nasal wall in *Eusthenopteron* has only an anterior, comparatively large opening, the fenestra endonarina anterior (p. 466; *fe. ena*, figs. 47, 67 A), whereas the corresponding wall in *Rana* is pierced by two openings, an anterior, fairly large fenestra endonarina communis (p. 311; *fe. en*, fig. 22 A—C), and a posterior much larger opening, the fenestra nasolateralis (p. 313; fig. 22 A—C). The latter is not confined to the lateral nasal wall only but also extends upwards in the tectum nasi. The lateral nasal wall is thus much more complete in *Eusthenopteron* than in *Rana*. As in this respect *Eusthenopteron* beyond doubt represents more primitive conditions than *Rana*, it follows that the lateral nasal wall in Anurans must have undergone a considerable reduction, resulting inter alia in the development of the fenestra nasolateralis. The primitive ancestors of the Anurans certainly had a fenestra endonarina anterior similar to that in *Eusthenopteron*, which, chiefly by the partial reduction of the lateral nasal wall, was modified into a fenestra endonarina communis. That these reductions and transformations have actually taken place and that as a result of them the nasolachrymal duct has undergone certain changes in its position in relation to the skeleton is demonstrated by the following facts.

1) In several Anurans, e. g. *Hyla*, *Breviceps*, *Liopelma* (see p. 316), the lateral nasal wall is much more complete than in *Rana*. In some of these forms the lamina obliqua is connected with the postnasal wall by a bridge of cartilage in much the same way as in the hypothetic primitive Anuran stage shown in fig. 67 B, and the fenestra nasolateralis is accordingly represented by two openings, a dorsal one in the tectum nasi (cf. fig. 67 B, *fe. te*) and a lower one in the posterior part of the lateral nasal wall. In addition, the processus maxillaris anterior in *Hyla* is connected anteriorly with the lamina nariochoanalis, so that the fenestra nasolateralis is closed ventrally. The posterior lateral parts of the nasal capsule in *Hyla* are fundamentally as in the hypothetic stage shown in fig. 67 B.

2) In certain Anurans (*Bombinator*, *Pelobates*, p. 316) the cartilaginous

bridge connecting the lamina obliqua with the postnasal wall is found in the larvae but not in the adults. A vestige of such a bridge is also present in larvae of *Rana*, where it forms but a small posterior process on the lamina obliqua (Gaupp 1893, pl. 14, fig. 24; Pusey 1938, pl. 34, figs. 3, 4; pl. 35, figs. 5, 6; cf fig. 67 C in this work). This shows plainly that a partial reduction of the lateral nasal wall takes place in the Anurans during their ontogenetic development.

3) The position and development of the lamina obliqua in Anurans are such that it must correspond to the portions of the lateral nasal wall in *Eusthenopteron* that lie above the notch *i. db* (p. 446; fig. 47) in the postero-ventral corner of the fenestra endonarina anterior and above that fenestra (see fig. 67), and its lowermost part is thickened quite as the lowermost part of those portions of the nasal capsule in *Eusthenopteron*, that is the part of the lateral nasal wall that bounds the notch *i. db* dorsally (cf. figs. 47 C, 52 A, B and Gaupp 1893, pl. 14, fig. 22). During the whole larval period of the Anurans the lamina obliqua is separated from the parts of the nasal capsule situated ventrally to it and only towards the end of the metamorphosis does it connect with the lamina inferior (Gaupp 1893, pp. 420, 421; pl. 14, figs. 22, 24). Owing to this the fenestra nasolateralis (or the equivalent of its lower part) is in larvae continuous anteriorly with the fenestra endonarina communis (cf. *fe. en*, fig. 67 B). The connection between the ventral thickened end of the lamina obliqua and the dorsal side of the lamina inferior is formed by the pars terminalis (*p. term*, fig. 22 A, C; p. 312), which develops within the nasal cavity on the medial side of the nasolachrymal duct. As there is no equivalent to it in *Eusthenopteron*, the pars terminalis must be regarded as a new formation in the Anurans (cf. foot-note 1 on p. 518).

4) The whole nasolacrymal duct (posterior external nasal tube) in *Eusthenopteron* (p. 467) lay within the nasal cavity along the lateral nasal wall and above both the posterior parts of the processus intermedius of the lamina nariochoanalis (*pr. im*, fig. 52 B) and the processus dermintermedius of the lateral rostral (*pr. dim*). The nasolachrymal duct in Anurans has secondarily, due to reductions and new formations of endoskeleton (see under 3 above), become situated outside the lateral nasal wall. It passes underneath the septomaxillary, which is homologous to the processus dermintermedius of the lateral rostral (see p. 535). In *Calyptocephalus* (p. 318) it has been found, however, that in larval stages it first lies dorsally to the septomaxillary, after which it "migrates" through that bone downwards, so that in adults it lies ventrally to it, as is usual in Anurans.

We may now assume that the lateral parts of the nasal capsule in

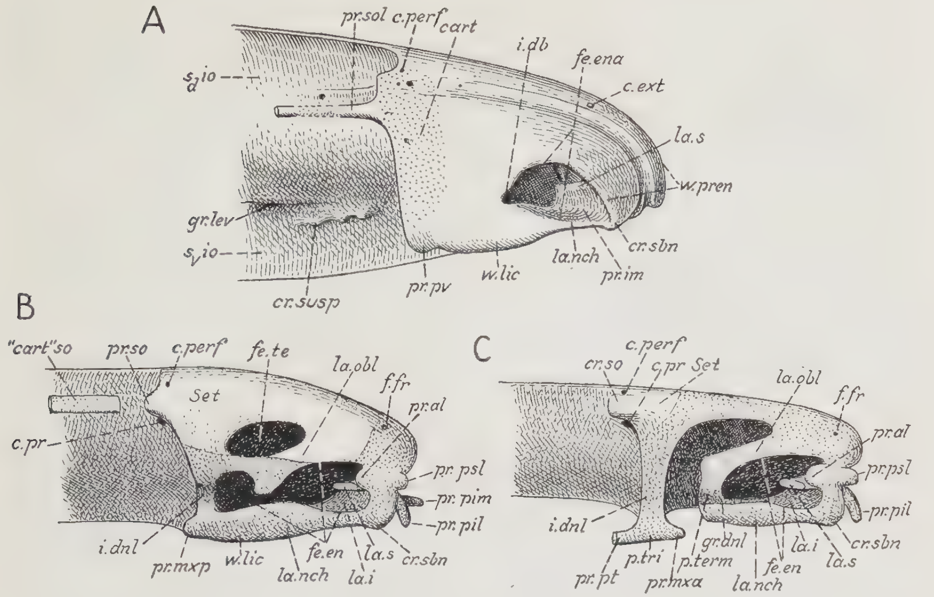
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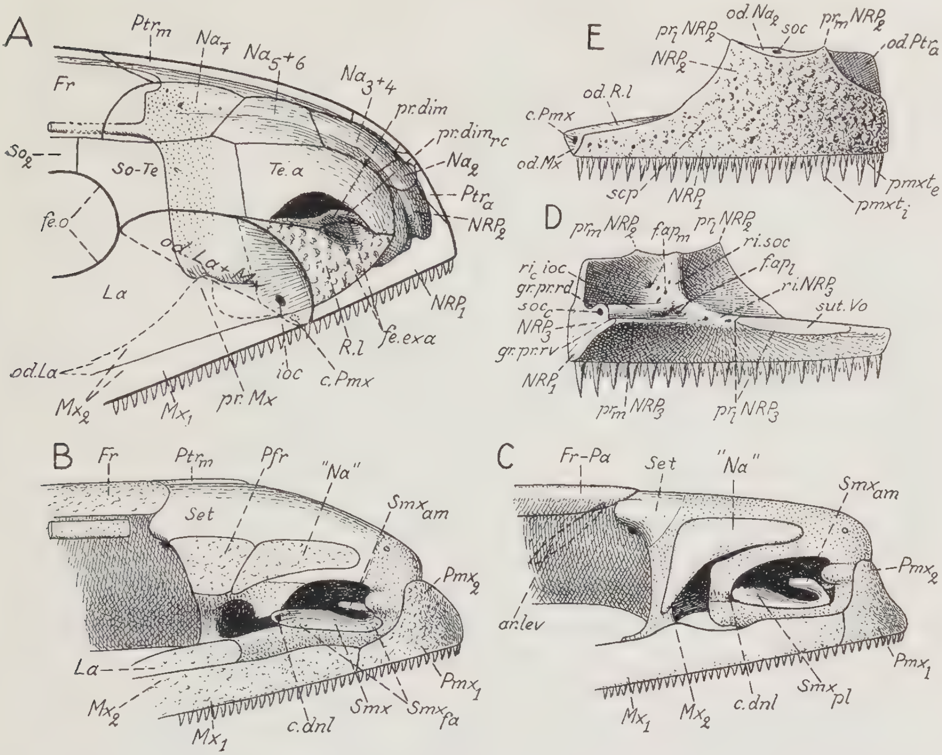
Fig. 67. Three drawings illustrating probable transformations in the lateral parts of the snout during the development of Anurans from Osteolepiform Crossopterygian ancestors. Endocranial parts in lateral aspect, the palatoquadrate omitted. Cartilage dotted. *A*, *Eusthenopteron foordi* Whiteaves. $^2/_1$. *B*, hypothetic very primitive Anuran stage of development. *C*, hypothetic stage more advanced than *B*.

Set, sphenethmoid; *cart,* part of endocranium, probably consisting of cartilage; *"cart"so,* "cartilago supraorbitalis", probably homologous to the posterior independent ossification of the processus supraorbitalis lateralis in *Eusthenopteron foordi*; *c. ext,* canal for r. externus narium of n. profundus; *c. perf,* canal for r. frontalis perforans of n. profundus; *c. pr,* profundus canal; *cr. sbn,* crista subnasalis; *cr. so,* crista supraorbitalis; *cr. susp,* crista suspendens; *fe. en,* fenestra endonarina communis; *fe. ena,* fenestra endonarina anterior; *fe. te,* opening in tectum nasi; *f. fr,* foramen frontale, corresponding to the canal *c. ext* in *Osteolepiformes*; *gr. lev,* groove for origin of principal portion of m. levator bulbi; *gr. dnl,* groove for ductus nasolacrimalis; *i. db,* notch for the processes of the anterior tectal and lateral rostral that extend into nasal cavity; *i. dnl,* incisure for ductus nasolacrimalis; *la. i,* lamina inferior; *la. nch,* lamina nariochoanalis; *la. obl,* lamina obliqua; *la. s,* lamina superior; *pr. al,* processus alaris; *pr. im,* processus intermedius of lamina nariochoanalis; *pr. mxa,* processus maxillaris anterior; *pr. mxp,* processus maxillaris posterior, homologous to the process *pr. pv* in *Osteolepiformes*; *pr. pil,* processus prenasalis inferior lateralis; *pr. pim,* processus prenasalis inferior medius; *pr. psl,* processus prenasalis superior lateralis; *pr. pt,* palatoquadrate bar ("processus pterygoideus"); *pr. pv,* postero-ventral process of ethmoidal region; *pr. so,* processus supraorbitalis, probably homologous to the thickened lateral part of lamina supraorbitalis in *Osteolepiformes*; *pr. sol,* processus supraorbitalis lateralis; *p. term,* pars terminalis; *p. tri,* pars triangularis; s_d*io,* s_v*io,* thin dorsal and ventral parts of interorbital wall; *w. lic,* ventral medially curved part of lateral nasal wall; *w. pren,* divisio prenasalis communis.

Anura have arisen from such parts of a *Eusthenopteron*-like form in about the following way (see fig. 67).

In connection with the reduction of the lateral parts of the postnasal wall, which transformed the fenestra endonarina posterior (*fe. enp*, fig. 65 A) into an incisure (*i. dnl*, figs. 65 B, C, 67 B, C, 70 B, C) for the nasolachrymal duct in the lateral margin of the postnasal wall (see p. 512), the adjacent hinder parts of the lateral nasal wall forwards to the postero-ventral corner (the notch *i. db*, fig. 67 A) of the fenestra endonarina anterior were probably also reduced. This caused a longitudinal opening in the lateral nasal wall outside and partly also above and below the nasolachrymal duct (posterior external nasal tube). Together with the fenestra endonarina anterior this new fenestration formed a continuous opening (*fe. en*, fig. 67 B) from the postnasal wall nearly to the prenasal wall, giving passage both to the anterior external nasal tube and to the nasolachrymal duct. Dorsally to the posterior parts of the opening just dealt with there arose another one (*fe. te*, fig. 67 B) in the upper part of the lateral nasal wall and in the adjacent part of the tectum nasi. An oblique skeletal bar, the lamina obliqua of the Anurans (*la. obl*, fig. 67 B), separated this opening from the anterior parts of the ventral one (*fe. en*) and projected downwards so as to divide the latter opening incompletely into two parts, anterior and posterior. A horizontal bridge which separated the dorsal opening (*fe. te*) from the hinder part of the ventral opening persisted. This bridge which like the oblique skeletal bar is a remainder of the primary lateral nasal wall persists in certain adult Anurans (*Hyla*, *Breviceps*, *Liopelma*) but is met with only in larvae of others (*Bombinator*, *Pelobates*). Simultaneously with the changes now discussed the nasolachrymal duct began to sink down into the processus dermintermedius of the lateral rostral (cf. pp. 537—539), so that it became enclosed in a canal (*c. dnl*, figs. 68 B, 70 B). The lateral rostral (*R. l*, fig. 68 A—C) was reduced except for its processus dermintermedius (*pr. dim*, $pr.\ dim_{rc}$) and a small dorsal part of the pars facialis (Smx_{fa}, figs. 68 B, 70 B). In connection with an extension forwards of the recessus medius (see p. 533 and fig. 72) the persisting parts of the lateral rostral were modified into a horseshoe-shaped bone (*Smx*, fig. 68 B), the septomaxillary of the Anurans (see pp. 529, 532—535). The remainder of the pars facialis (Smx_{fa}), which retained its primary position outside the nasal cavity, is the external lamina of the septomaxillary in certain Anurans (cf. p. 318).

Through these hypothetic modifications and through others dealt with above (pp. 508—509) the ethmoidal region may be assumed to have reached a very primitive Anuran stage (cf. figs. 64 B, 65 B, 67 B, 70 B, 71 B, 72 B). During the following development, which took place within the group *Anura*, the lateral parts of the nasal capsule may be supposed to have undergone the following changes. The bridge of endoskeleton separating the upper opening (*fe. te*) from the posterior part of the lower opening (*fe. en*, fig. 67 B) generally disappeared completely, so that a continuous large opening, the fenestra nasolateralis, was formed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Mx_1
Mx_2

Fig. 68. *A—C*, three drawings illustrating the modifications which presumably took place in the dermal bones of the lateral parts of the snout during the development of Anurans from Osteolepiform Crossopterygian ancestors. The snout seen from the lateral side. Cartilage dotted. *A*, *Eusthenopteron foordi* Whiteaves. In order to show their position in relation to the endocranium, all the dermal bones, except the lateral rostral, shown in outline only. Extent of certain overlapped parts of bones indicated by broken lines. $^2/_1$. *B*, hypothetic very primitive Anuran stage. *C*, somewhat more advanced Anuran stage. *D*, *E*, *Eusthenopteron foordi* Whiteaves. Naso-rostro-premaxillary in, *D*, internal and, *E*, external views. Restorations based on several specimens. $^8/_3$.

Fr, frontal; *Fr-Pa*, fronto-parietal; *La*, lachrymal; Mx_1, Mx_2, pars dentalis and pars facialis of maxillary; "*Na*", Anuran nasal, probably homologous to the anterior tectal in *Osteolepiformes*; Na_2, nasal 2; Na_{3+4}, compound nasal formed by fusion of nasals 3 and 4; Na_{5+6}, compound nasal formed by fusion of nasals 5 and 6; Na_7, nasal 7; NRP_1, NRP_2, NRP_3, pars dentalis, pars facialis and pars palatina of naso-rostro-premaxillary; *Pfr*, prefrontal, probably homologous to the supraorbito-tectal in *Osteolepiformes*; Pmx_1, Pmx_2, pars dentalis and pars facialis of the Anuran premaxillary; Ptr_a, anterior median postrostral; Ptr_m, posterior median postrostral; *R. l*, lateral rostral; *Set*, sphenethmoid; *Smx*, septomaxillary, homologous to the lateral rostral in *Osteolepiformes*; Smx_{am}, antero-medial shank of septomaxillary, homologous to antero-medio-dorsal recurved portion of processus dermintermedius of lateral rostral in *Osteolepiformes*; Smx_{fa}, external lamina of septomaxillary, corresponding to facial part of lateral rostral in *Osteolepiformes*; Smx_{pl}, postero-lateral shank of septomaxillary, homologous to posterior horizontal and middle main portions of processus dermintermedius in *Osteolepiformes*; *So-Te*, supraorbito-tectal; So_2, posterior supraorbital; *Te. a*, anterior tectal; *ar. lev*, place of origin of principal portion of m. levator bulbi; *c. dnl*, canal for ductus nasolacrimalis; *c. Pmx*, canal for nerve to premaxillary teeth; $f.\ ap_l$, $f.\ ap_m$, foramina for rr. apicales of r. me-

(fig. 67 C). Certain ventral portions of the lateral nasal wall ventrally to the posterior part of the lower opening (*fe. en*, fig. 67 B), between this and the fenestra endochoanalis, normally disappeared at very much the same time (exception: *Hyla*), so that the fenestra nasolateralis became continuous ventrally with the fenestra endochoanalis. A hindmost ventral portion of the lateral nasal wall persisted as an anteriorly directed process from the postnasal wall, the processus maxillaris anterior of the Anurans (*pr. mxa*, figs. 22 A, D, 67 C, 70 C; p. 314), and the part of the ethmoidal region from which it issues represented the pars triangularis (*p. tri*, figs. 67 C, 70 C). The processus maxillaris anterior and the anterior part of the pars triangularis retained a medial curve and relations to the recessus lateralis of the nasal cavity corresponding to those of the posterior ventral part (*w. lic*, fig. 67 A) of the lateral nasal wall in *Eusthenopteron* (see p. 441). The nasolachrymal duct shifted further downwards through the hinder part of the septomaxillary so as ultimately to be situated ventrally to that bone, in a space which arose by the reduction of an upper part of the processus intermedius and constituted a new formation incorporated into the recessus medius (*re. med*, figs. 71 B, C, 72 B, C; see p. 533). The middle main and posterior horizontal portions of the processus intermedius (*pr. im*, $pr.\,im_h$, figs. 47, 52, 67 A, 70 A) decreased in thickness and were modified into the lamina inferior (*la. i*, figs. 22 A, C, E, 67 C) of the Anurans (see p. 534). An at least partly new formation of cartilage medially to the nasolachrymal duct, the pars terminalis of the Anurans (*p. term*, fig. 22 A, C, E, 67 C), connected the ventral end of the lamina obliqua (*la. obl*, fig. 67 B, C) with the lamina inferior and separated the fenestra endonarina communis (*fe. en*, fig. 67 C) from the fenestra nasolateralis[1]. The pars terminalis was connected with the lamina inferior somewhat medially to the upper margin of the lamina nariochoanalis (*la. nch*, fig. 67 C), and thus a rostro-caudal groove (*gr. dnl*, figs. 22 A, C, 67 C) for the nasolachrymal duct arose here between the fenestra endonarina communis and the fenestra nasolateralis. The anterior part of this groove was covered by the septomaxillary, so that the nasolachrymal duct (*dnl*, fig. 29) became situated in a short canal (*c. dnl*, fig. 68 C; cf. fig. 29; pp. 311, 318). In connection with the modifications through which the fenestra endonarina communis gained its posterior boundary, the recessus superior of the nasal cavity widened in a forward direction through a partial reduction of the prenasal wall (see p. 534). The lateral wall of this widened recess was then partly reduced and a posterior process, the processus alaris (*pr. al*, figs. 22 A—E, 67 B, C, 69, 70 B, C, 71 B, C), projecting backwards in the fenestra endonarina communis was formed.

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[1] The upper portion of the pars terminalis is certainly a new formation, but its lower portion presumably corresponds to the postero-medial part of the horizontal portion of the processus intermedius in *Eusthenopteron*.

dialis narium of n. profundus; *fe. exa*, fenestra exonarina anterior; *fe. o*, orbital opening; *gr. pr. rd*, *gr. pr. rv*, grooves for dorsal and ventral rostral processes; *ioc*, infraorbital sensory canal; *od. La*, area of maxillary overlapped by lachrymal; $od.\,La+Mx$, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *od. Mx*, area overlapped by maxillary; $od.\,Na_2$, area overlapped by nasal 2; $od.\,Ptr_a$, area overlapped by anterior median postrostral; *od. R. l*, area overlapped by lateral rostral; $pmxt_e$, $pmxt_i$, external and internal rows of premaxillary teeth; *pr. dim*, processus dermintermedius of lateral rostral; $pr.\,dim_{rc}$, antero-medio-dorsal recurved portion of processus dermintermedius; *pr. Mx*, dorsal process of maxillary; $pr_l NRP_2$, $pr_m NRP_2$, lateral and medial processes of pars facialis of naso-rostro-premaxillary; $pr_l NRP_3$, $pr_m NRP_3$, lateral and medial processes of pars palatina of naso-rostro-premaxillary; $ri_c ioc$, ridge lodging ethmoidal commissure of infraorbital sensory canals; $ri.\,NRP_3$, dorsal ridge of pars palatina of naso-rostro-premaxillary; *ri. soc*, supraorbital sensory canal ridge; *scp*, pores of sensory canals; *soc*, supraorbital sensory canal; soc_c, ethmoidal commissure of infraorbital sensory canals; *sut. Vo*, area in sutural connection with vomer.

As may be gathered from the above, the lateral nasal wall in *Eusthenopteron* chiefly differs from the corresponding nasal wall in Anurans by being much more completely developed. If, as we have assumed, certain parts of it were reduced, it would be almost exactly as in Anurans, and it is thus obvious that it may easily have been modified into a lateral nasal wall of an Anuran type.

The prenasal wall is considerably thicker in *Eusthenopteron* (p. 443; *w. a*, figs. 47 A, B, 57 B, 59; *w. pren*, figs. 71 A, 72 A) than in the *Anura*, where it normally forms a thin transverse lamina (*w. a*, fig. 72 C; cf. figs. 22 A—C, E, 30, 67 B, C, 70 B, C, 71 B, C, 72 B) between the nasal cavity and the lateral part of the cavum prenasale. Through partial reductions 1) of its most anterior part in connection with the transformation of the prenasal pits into the cavum prenasale (see pp. 502—503) and 2) of its most posterior part in connection with a widening forwards of the nasal cavity (see pp. 527—535), the prenasal wall in *Eusthenopteron* may, however, easily be modified into a prenasal wall of an Anuran type (figs. 67, 70, 72).

The solum nasi (*sol. n*) is very similar in *Eusthenopteron* (pp. 445—446; figs. 47 C, 48, 51—53) and *Rana* (p. 313, figs. 22 A—D, 27 B), in both being formed by a fairly narrow ledge along the ventral margins of the prenasal and internasal walls. The fact that this ledge is somewhat broader in *Rana* than in *Eusthenopteron* and antero-laterally reaches the lateral nasal wall is due to the condition that the nasal cavity in Anurans extends slightly farther medially and forwards (see pp. 527, 530—535) than in *Eusthenopteron*. The crest (*cr. em*, figs. 22 A, 27 B; p. 313) in *Rana* supporting the eminentia olfactoria has no equivalent in *Eusthenopteron*.

The fenestra endochoanalis (*fe. ench*) is developed very much in the same way in *Eusthenopteron* (figs. 48, 51, 52 A, 53, 64 A, 70 A; pp. 447—448) and *Rana* (figs. 22 A, D, 23 B; pp. 313—314). In both it is a large opening occupying the larger posterior and lateral parts of the solum nasi. Its lateral and posterior boundaries are formed by the lateral nasal wall and postnasal wall respectively. In *Rana* a portion of the lateral nasal wall is normally absent so that the fenestra in question is continuous dorso-laterally with the fenestra nasolateralis (cf. p. 518 and figs. 67, 70). The lowermost part of the postnasal wall forming the posterior boundary of the fenestra in question in *Rana*, and in Anurans in general, presumably includes a portion of the palatoquadrate (the commissura quadrato-cranialis anterior) corresponding to the antero-lateral part of the pars autopalatina in *Eusthenopteron* (see pp. 520—525). The fenestra endochoanalis in Anurans is therefore probably homologous to the opening in *Eusthenopteron* that is bounded postero medially by the pars autopalatina of the palatoquadrate (see fig. 64 A).

The palatoquadrate bar in larvae of *Rana* and other Anurans (figs. 25, 26; pp. 319—322) is fairly broad and connected by a powerful antero-medial process, the commissura quadrato-cranialis anterior (*com. qca*), with the endocranium, at the angle between the interorbital wall and the embryonic postnasal wall, the lamina orbitonasalis (*la. on*). The commissura is practically transverse in position and is situated so that its anterior margin is close below the lamina orbitonasalis. The lateral part of the anterior margin of the commissura is provided with a small process, the antero-lateral process or processus quadrato-ethmoidalis (*pr. qe*), which points antero-dorso-laterally and whose apex rests against the processus maxillaris posterior (*pr. mxp*; cf. figs. 65 B, 67 B) of the lamina orbitonasalis. The postero-lateral part of the commissura quadrato-cranialis anterior and the adjacent part of the palatoquadrate bar bears a thin lamina of varying size, the processus pseudopterygoideus (*pr. pspt*), which projects backwards and somewhat medially into the fenestra subocularis (*fe. sboc*). In *Eusthenopteron* (figs. 54—56, 64 A, 65 A, 70 A; pp. 451—453) the foremost part of the palatoquadrate, the pars autopalatina, is much more strongly developed than in larvae of *Rana*. Antero-medially its medial ethmoidal articular area (art_2m) has a rigid, probably even synchondrotic connection with the medial autopalatine articular area (art_1m, figs. 48—50, 65 A), which is situated on the endocranium at the angle between the postnasal and interorbital walls. Laterally to this connection the pars autopalatina abuts with its antero-lateral margin (the lateral ethmoidal articular area, art_2l) against the ventral margin (the lateral autopalatine area, art_1l) of the postnasal wall. The lateral articular area of the pars autopalatina presents a low dorsal

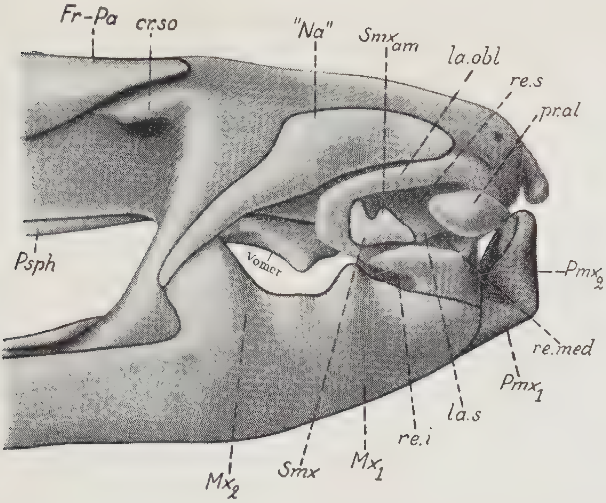


Fig. 69. *Rana fusca.* The skeleton of the snout of a young individual in lateral view. From ECKER-WIEDERSHEIM-GAUPP (1904, fig. 147). $^{20}/_{1}$.

Fr-Pa, fronto-parietal; Mx_1, Mx_2, pars dentalis and pars facialis of maxillary; "*Na*", "nasal"; Pmx_1, Pmx_2, pars dentalis and pars facialis of "premaxillary"; *Psph*, parasphenoid; *Smx*, septomaxillary; Smx_{am}, antero-medial shank of septomaxillary; *cr. so*, crista supraorbitalis; *la. obl*, lamina obliqua; *la. s*, lamina superior; *pr. al*, processus alaris; *re. i*, *re. med*, *re. s*, recessus inferior, recessus medius and recessus superior of nasal cavity.

process, the processus dorso-lateralis (*pr. dl*), lying just medially to and abutting against the medial side of the ventro-lateral corner of the postnasal wall, which forms a small postero-ventral process (*pr. pv*, figs. 48—50, 65 A, 67 A). The relations between the foremost part of the palatoquadrate and the endocranium thus show important points of agreement in *Eusthenopteron* and *Rana* (cf. figs. 64, 65, 70). The connection between the commissura quadrato-cranialis arterior and the endocranium in larvae of Anurans corresponds to the probably synchondrotic connection between the medial ethmoidal (art_2m) and medial autopalatine (art_1m) articular areas in *Eusthenopteron*. The processus quadrato-ethmoidalis (*pr. qe*) in larvae of Anurans is exactly as the dorso-lateral process (*pr. dl*) of the pars autopalatina in *Eusthenopteron*. The processus maxillaris posterior (*pr. mxp*) in larvae of Anurans has the same relations to the palatoquadrate as the postero-ventral process (*pr. pv*) of the ethmoidal region in *Eusthenopteron*. The agreement is thus so detailed that it can hardly be explained as a parallelism. We may therefore be justified in concluding: 1) That the commissura quadrato-cranialis anterior with its processus quadrato-ethmoidalis (*pr. qe*) is the homologue of the foremost and antero-lateral parts of the pars autopalatina in *Eusthenopteron* backwards approximately to the ridge *ri. lev* (see figs. 65 A, 70 A), i. e. of those thickened parts of the pars autopalatina which bear the medial (*art₂m*) and lateral (*art₂l*) ethmoidal articular areas and the dorso-lateral process (*pr. dl*); and 2) that the lamina orbitonasalis in larvae of Anurans ("planum antorbitale primarium" REINBACH) with its processus maxillaris posterior (*pr. mxp*) is the homologue of the postnasal wall in *Eusthenopteron* with its postero-ventral process (*pr. pv*; cf. fig. 65 A, B).

No equivalents to the medial and postero-medial parts of the pars autopalatina of the palatoquadrate in *Eusthenopteron* are found in *Rana*, and consequently this form displays no traces of the connection developed in *Eusthenopteron* between the medial parts of the pars autopalatina and the endocranium (the crista suspendens and the pits *fo. pr. dm* and *fo. cr. vm*; cf. pp. 454—456). Presumably equivalents to the medial and postero-medial parts of the pars autopalatina in *Eusthenopteron* were primarily present in the ancestors of *Rana* and must have become reduced together with the other medial parts of the palatoquadrate in consequence of the development of the wide fenestra subocularis. It is easily seen that if the medial and postero-medial parts of the pars autopalatina in *Eusthenopteron* were reduced (see figs. 64, 65, 70), the remaining anterior and lateral parts would be almost exactly as the commissura quadratocranialis anterior and the anterior part of the palatoquadrate bar in larvae of *Rana*. It is also easily seen that the processus pseudopterygoideus in larvae of Anurans may be a remainder of a middle portion (*pr. pspt*, figs. 64 B, 65 B, 70 B) of the pars autopalatina in *Eusthenopteron*.

The opinions now expressed as to the homologies of the foremost part of the palatoquadrate bar in larvae of Anurans and the modifications that have taken place in the foremost part of the palatoquadrate in Anurans are supported also by the following facts.

1) The dermopalatine in *Eusthenopteron* (*Dpl.* figs. 64 A, 65 A) is a dermal bone developed on the lower side of the part of the palatoquadrate interpreted above as corresponding to the commissura quadratocranialis anterior in larvae of Anurans. The dermopalatine in *Rana* according to ERDMANN (1933, pp. 608—609; cf. REINBACH 1939, p. 332; pl. 15, fig. 6) arises ontogenetically in connection with the commissura quadratocranialis anterior (cf. figs. 64 B, 65 B, C). The position of this bone in relation to the palatoquadrate thus corroborates the homologation of the commissura quadrato-cranialis anterior in larvae of Anurans with the anterior and antero-lateral parts of the pars autopalatina in *Eusthenopteron*.

2) In *Eusthenopteron* the postchoanal nerve anastomosis (*ast. pch*) and the r. palatonasalis (*r. p-n*; fig. 60; p. 477) passed close antero-laterally to the processus dorso-lateralis (*pr. dl*) of the pars autopalatina and thus

morphologically laterally to the connection between this process and the processus postero-ventralis (*pr. pv*) of the postnasal wall. In larvae of Anurans (*Calyptocephalus*, fig. 25 B; pp. 332—333) the said two nerves have a corresponding course in relation to the processus quadrato-ethmoidalis and to the connection between that process and the processus maxillaris posterior.

3) In the larvae of certain Anurans, e. g. *Pseudis* (W. K. PARKER 1881, pl. 11, figs. 1, 2) and *Xenopus* (KOTTHAUS 1933, fig. 18; PATERSON 1939, pl. 13, figs. 22, 23; pl. 14, fig. 24), the palatoquadrate bar is considerably broader and the commissura quadrato-cranialis anterior extends further backwards than in *Rana*. As a result the fenestra subocularis in *Pseudis* and *Xenopus* is comparatively small and the foremost part of the palatoquadrate in these two forms is therefore far more similar to the pars autopalatina in *Eusthenopteron* than it is in *Rana*.

4) In certain specimens of *Eusthenopteron* (F. 5 in PATTEN's Collection) only the foremost and lateral parts of the pars autopalatina are ossified, i. e. the very parts of the pars autopalatina that would correspond to the commissura quadrato-cranialis anterior and the adjacent part of the palatoquadrate bar in larvae of Anurans. In the specimen of *Eusthenopteron* used for grinding-series 2 the postero-medial part of the pars autopalatina was delicate and fenestrated (*fe. pq*, figs. 54 B, 55). There are thus even in *Eusthenopteron* indications of an initial reduction of the medial and postero-medial parts of the pars autopalatina.

The changes that the anterior part of the palatoquadrate undergoes in Anurans during the later phase of the metamorphosis are very differently interpreted by GAUPP, PUSEY and most other writers on the one hand and by REINBACH on the other (see pp. 319—322). According to GAUPP and PUSEY, the commissura quadrato-cranialis anterior is absent in adult Anurans, with the exception of the most lateral part bearing the processus quadrato-ethmoidalis. The processus maxillaris posterior of the postnasal wall has grown out excessively in a posterior direction and the persisting part of the commissura has been pushed backwards so as to enter into the formation of the posterior parts only of the palatoquadrate. The postnasal wall in adult Anurans according to this interpretation is formed only by the lamina orbitonasalis and thus represents solely the postnasal wall in Osteolepiform Crossopterygians. According to REINBACH, on the other hand, the commissura quadrato-cranialis anterior of the larvae persists as a whole in the adults, in which it is fused with the lamina orbitonasalis ("planum antorbitale primarium"), and the postnasal wall ("planum antorbitale secundarium") of adult Anurans is thus a complex formation including the homologues both of the postnasal wall and of the anterior and antero-lateral parts of the pars autopalatina of Osteolepiform Crossopterygians.

Reinbach's interpretation of the postnasal wall in adult Anurans is supported by its relations to the dermopalatine and the m. levator bulbi.

The dermopalatine in fishes in general is a dermal bone developed in relation to the foremost part of the palatoquadrate. In *Eusthenopteron* (*Dpl*, figs. 54—56, 64 A, 65 A; pp. 453—454) it is situated on the lower side of that part of the pars autopalatina of the palatoquadrate which, as demonstrated above, corresponds to the commissura quadrato-cranialis anterior in larvae of Anurans. In adult Anurans, on the other hand, it covers the ventral face of the postnasal wall (*Dpl*, figs. 23, 66; cf. figs. 64 B, 65 B, C). That this is so in adult Anurans is easily accounted for if it is assumed that the commissura quadrato-cranialis anterior as a whole is incorporated in the lowermost part of the postnasal wall. The dermopalatine has then retained its primary position in relation to the pars autopalatina. If, on the other hand, the commissura quadrato-cranialis anterior had been almost entirely reduced and pushed far backwards, we must assume that the dermopalatine secondarily has been associated with the ventral margin of the postnasal wall.

When the palatoquadrate in *Eusthenopteron* is in position in relation to the endocranium, we find between its anterior end and the postnasal wall a deep but small pit, *fo. p. tr* (figs. 55, 65 A; p. 456). Presumably a muscle was inserted into it and into the adjacent part of the pars autopalatina. Since the oblique muscles of the eye arose in another place (see pp. 511—512), this pit was probably caused by a muscle corresponding to a portion of the m. levator bulbi in Anurans. In *Pelobates* the m. levator bulbi has a portio transversalis (Luther 1914, p. 26, figs. 17—20), which is vestigial in *Rana*. In *Pelobates* the portio transversalis arises from the lateral face of the interorbital wall medially to and somewhat above the n. profundus, and its postero-dorsal part thus lies medially to that nerve. From there it extends forwards, laterally and downwards and gradually becomes rounded in section towards its ventral end. In larvae it is inserted into the upper side of the commissura quadrato-cranialis anterior, in adults, on the other hand, into the posterior face of the postnasal wall. A muscle corresponding to that portion in *Pelobates* may be supposed to have been inserted in *Eusthenopteron* into the pit *fo. p. tr* and into the adjacent part of the pars autopalatina. This muscle in *Eusthenopteron* may have arisen in the depression on the lateral side of the olfactory ridge (fig. 65 A; p. 436). The principal portion of the m. levator bulbi in *Rana* (*m. lev. b*, figs. 30, 31; Ecker-Wiedersheim-Gaupp 1904, pp. 895—900; figs. 231, 238—240) arises from an area on the interorbital wall (cf. fig. 68 C, *ar. lev*) which extends from the neighbourhood of the hinder orifice of the profundus canal obliquely downwards and backwards to a spot somewhat ventrally to the opticus foramen. In larvae this portion is inserted into the palatoquadrate (see Luther 1914, fig. 22) but in adults inter alia into the ventral margin of the postnasal wall. Also this portion of the m. levator bulbi was probably present in *Eusthenopteron* and may have arisen in the groove *gr. lev* (figs. 47 B, 48—50, 55, 67 A; p. 439) on the lower side of the olfactory ridge and had its insertion into the ridge *ri. lev* (figs. 54 B, 55, 65 A, 70 A; p. 451) on the upper side of the part of the pars autopalatina that seems to be the true homologue of the commissura quadrato-cranialis anterior in Anurans. In the ancestors of the Anurans both the portio transversalis and the principal portion of the m. levator bulbi must have been inserted into the foremost part of the palatoquadrate. The fact that in adult Anurans these two muscles are instead inserted into the postnasal wall is quite natural under the assumption that the commissura quadrato-cranialis anterior is incorporated in the postnasal wall, but it is more difficult to understand if the commissura quadrato-cranialis anterior is largely reduced and does not enter into the formation of the postnasal wall. In the latter case we are forced to assume that the insertions of the two muscles migrate dorsally during the ontogenetic development of the Anurans, moving from the palatoquadrate to the postnasal wall (cf. Luther 1914, p. 26).

As far as I can see, there are thus great reasons to believe that the postnasal wall in adult Anurans is a complex formation including both the primary postnasal wall and a palatoquadrate component corresponding to the anterior and the antero-lateral parts of the pars autopalatina of Osteolepiform Crossopterygians.

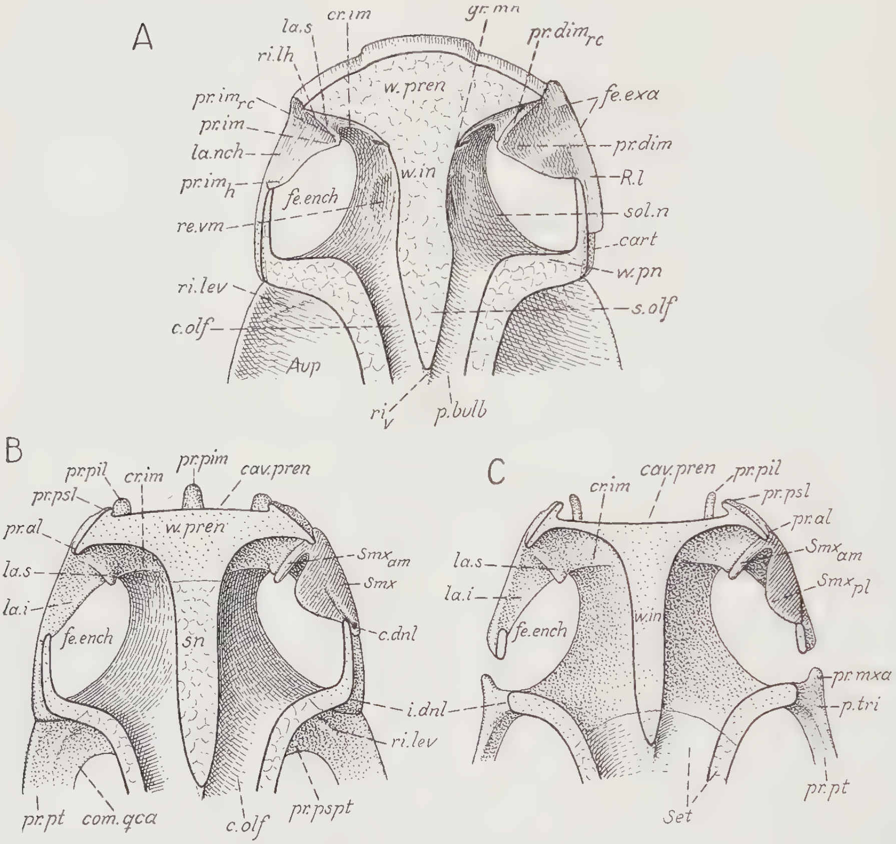
Pusey (1938, pp. 528—529) has advanced the opinion that the commissura quadrato-cranialis anterior in *Rana* "is the basal process of the quadrate which has passed exceptionally far forward to fuse with the trabecula just behind the nasal sac". The commissura quadrato-cranialis anterior is, however, as has been demonstrated here, in all probability the true equivalent of the anterior and antero-lateral parts of the pars autopalatina in *Eusthenopteron*. Since there is in *Eusthenopteron* a true homologue of a basal process further caudally on the palatoquadrate (cf. p. 494; cf. also Watson 1926, pp. 248—249; Holmgren and Stensiö 1936, p. 353; Stadtmüller 1936, p. 577), Pusey's opinion as to the homology of the commissura quadrato-cranialis anterior cannot possibly be true. This is also borne out by the fact that the palatoquadrate in Stegocephalians probably had both a basal process and an anterior portion equivalent to the commissura quadrato-cranialis anterior in Anurans (Säve-Söderbergh 1936; p. 166; Watson 1940, p. 226; fig. 23).

The endoskeleton of the snout is but slightly ossified in *Rana*. The foremost part of the palatoquadrate is entirely cartilaginous, but the hinder median part of the ethmoidal region and the adjacent anterior part of the interorbital wall is formed by an unpaired ossification, the sphenethmoid bone (*Set*, figs. 23, 24; cf. fig. 66; pp. 308—309). The ossification of the endocranial parts of the snout in other Anurans is on the whole as in *Rana*. However, in certain forms, such as *Hemisus* (p. 317), the sphenethmoid bone may extend much further forwards than in *Rana*, occupying the larger part of the postnasal walls, the whole septum nasi and also adjacent parts of the tectum and solum nasi. In *Hemisus* only the foremost and antero-lateral parts of the ethmoidal region are thus made up of cartilage. In *Eusthenopteron* the interorbital wall and ethmoidal region are occupied throughout by the large unpaired ethmosphenoid bone (*Etsph*, fig. 34; pl. 10), but, as we have seen (p. 427), both the postero-dorso-lateral parts of the ethmoidal region (*cart*, figs. 47, 65 A, 67 A) and the lamina nariochoanalis sometimes remained unossified in this form. In the latter case the degree of ossification of the ethmoidal region is thus not very different in *Eusthenopteron* and in *Hemisus*. The palatoquadrate in *Eusthenopteron* is mostly well ossified, but in certain individuals the medial parts of the pars autopalatina may be unossified or fenestrated (see p. 523, No. 4). In *Eusthenopteron* there are thus indications of an initial reduction of the antero-lateral and lateral parts of the ethmoidal region and of the antero-medial part of the palatoquadrate. If this reduction had proceeded further backwards towards the hinder and median parts of the ethmoidal region and the bone tissue in the anterior parts of the palatoquadrate had also disappeared, the ossification of the endoskeleton of the snout in *Eusthenopteron* would be fundamentally as in Anurans (see figs. 64, 65, 67, 70—72).

The nasal cavity has on the whole a very similar position in *Eusthenopteron* (pp. 464—467; figs. 51—53, 57, 59, 70 A, 71 A) and *Rana* (pp. 309—313; figs. 22 A, C, D, 27, 30), separated from that of the opposite side by a more or less thin solid nasal septum (*sn*). As regards the structure of this cavity the two forms also display many fundamental points of agreement.

The horizontal crest in the nasal cavity in *Eusthenopteron* described as the crista intermedia (*cr.im*, figs. 52 A, C, 70 A; p. 445) has such a position and such relations (cf. pp. 541—542) that it must be homologous to the crista intermedia in Anurans (fig. 22 A, C, E; p. 312). By this crista the antero-medial part of the nasal cavity is subdivided both in *Eusthenopteron* and *Rana* into a dorsal and a ventral compartment, constituting the medial parts of the recessus superior (*re. s*) and recessus inferior (*re. i*). The difference between *Eusthenopteron* and *Rana* as to the development of the antero-medial part of the nasal cavity is chiefly that the medial parts of the superior and inferior recesses do not extend so far forwards in *Eusthenopteron* as in *Rana* and that, correlative with this, the crista intermedia does not extend so far rostro-caudally in *Eusthenopteron* as in *Rana*. In this respect *Eusthenopteron* is somewhat more primitive than *Rana* and it is readily seen (figs. 70, 71) that a widening of the medial parts of the recessus superior and recessus inferior in an anterior direction combined with certain reductions of the posterior parts of the divisio prenasalis communis would result in conditions quite similar to those in *Rana* (fig. 22 C; cf. fig. 22 E). The crista intermedia would be more prominent. The hinder portion of the nasobasal canal (*c. n-b*) would disappear and this together with the reduction of its anterior parts in connection with the development of the cavum prenasale (p. 503) would transform the canal into a foramen, the fenestra nasobasalis (*fe. n-b*, fig. 71 B, C), through which the recessus inferior would be in communication with the cavum prenasale. If the nasal cavity as a whole in *Eusthenopteron* were somewhat widened also in a medial direction through a reduction of the lateral parts of the nasal septum, this septum would become narrower and more like that in *Rana*. The ventro-medial recess (*re. vm*, figs. 70 A, 71 A) and the groove for the r. medialis narium (*gr. mn*) would then also disappear and the conditions in the medial parts of the nasal cavity would thus be exactly as in *Rana* and other Anurans. Moreover, the canal for the r. externus narium (p. 470; *c. ext*, figs. 47 B, 67 A, 71 A) would be shortened and would pierce the antero-medial part of the tectum nasi just as the foramen for the corresponding nerve-branch (see pp. 541—542), the foramen frontale (p. 311; *f. fr*, figs. 22 A—C, 29, 30; cf. figs. 67 B, C, 71 B, C), does in *Rana*. Further reductions of the antero-medial superficial parts of the ethmoidal region (see fig. 71) may then easily shorten the canal to a mere foramen corresponding exactly to the foramen frontale in *Rana*.

The antero-lateral part of the nasal cavity both in *Rana* (pp. 312—313, fig. 22 A, C) and in *Eusthenopteron* (pp. 464—466, figs. 52, 53, 57 A—D, 70 A, 71 A, 72 A) is much more complicated than the antero-medial part. Laterally the crista intermedia in *Rana* passes over into two laminae, the lamina superior (*la. s*) and the lamina inferior (*la. i*), of which the latter is continuous anteriorly with the prenasal wall, whereas the lamina superior has a free anterior margin. In certain other Anurans (*Arthroleptides*, *Calyptocephalus*, p. 316; fig. 22 E), however, the lamina superior passes over anteriorly into the prenasal wall.


A
la.s
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pr.mxa
p.tri
pr.pt
Set

Fig. 70. Three drawings illustrating the probable transformations in the ethmoidal region and palatoquadrate during the development of Anurans from Osteolepiform Crossopterygian ancestors. The endoskeleton in dorsal aspect, with the dorsal parts removed by a horizontal section. The lateral rostral (septomaxillary) shown on the right side in its relation to the endoskeleton. Cartilage-bone reticulate in section. Cartilage dotted. *A*, *Eusthenopteron foordi* Whiteaves. $^2/_1$. *B*, hypothetic primitive Anuran stage. *C*, hypothetic somewhat more advanced Anuran stage.

Aup, pars autopalatina; *R. l*, lateral rostral; *Set*, sphenethmoid; *Smx*, septomaxillary, homologous to lateral rostral in *Osteolepiformes*; Smx_{am}, Smx_{pl}, antero-medial and postero-lateral shanks of septomaxillary, homologous to the antero-medio-dorsal recurved and to the middle main and posterior horizontal portions resp. of the processus dermintermedius in *Osteolepiformes*; *cart*, part of endocranium, probably made up of cartilage; *cav. pren*, cavum prenasale; *c. dnl*, canal for ductus nasolacrimalis; *c. olf*, canalis olfactorius; *com. qca*, commissura quadrato-cranialis anterior; *cr. im*, crista intermedia; *fe. ench*, fenestra endochoanalis; *fe. exa*, fenestra exonarina anterior: *gr. mn*, groove for r. medialis narium of n. profundus; *i. dnl*, notch for ductus nasolacrimalis; *la. i*, lamina inferior; *la. nch*, lamina nariochoanalis; *la. s*, lamina superior; *p. bulb*, bulbar portion of cranial cavity; *pr. al*, processus alaris; *pr. dim*, processus dermintermedius of lateral rostral; $pr.\ dim_{rc}$, antero-medio-dorsal recurved portion of processus dermintermedius; *pr. im*, processus intermedius of lamina nariochoanalis; $pr.\ im_{h}$, posterior horizontal portion of processus intermedius; $pr.\ im_{rc}$, antero-medio-dorsal recurved portion of processus intermedius; *pr. mxa*, processus maxillaris anterior; *pr. pil*, processus prenasalis inferior lateralis; *pr. pim*, processus prenasalis inferior medius; *pr. psl*, processus prenasalis superior lateralis; *pr. pspt*, processus pseudopterygoideus; *pr. pt*, palatoquadrate bar ("processus ptery-

In *Eusthenopteron* we also find two laminae in the antero-lateral part of the nasal cavity, one dorsal and one ventral, which extend backwards from the prenasal wall. The dorsal one of these two laminae, the lamina superior (*la. s*, p. 443), is formed by the lateral horizontal ridge (*ri. lh*) on the posterior face of the prenasal wall (p. 443) and the antero-medio-dorsal recurved portion ($pr.\ im_{rc}$) of the processus intermedius (pp. 442—443). Both in *Eusthenopteron* and in *Rana* the lamina superior passes over medially into the crista intermedia, but goes further backwards than that, about to the middle of the anterior half (*Eusthenopteron*) or to the middle of the posterior part of the anterior half (*Rana*) of the nasal cavity[1], where it ends in a distinct corner or apex. Along the free postero-lateral margin of the lamina superior lies a portion of a dermal bone, viz. the antero-medial shank of the septomaxillary (pp. 317—318; Smx_{am}, fig. 69; cf. figs. 68 C, 70 C, 71 C, 72 C; *Smx*, fig. 29) in *Rana* and the antero-medio-dorsal recurved portion ($pr.\ dim_{rc}$, figs. 68 A, 70 A, 71 A, 72 A) of the processus dermintermedius of the lateral rostral in *Eusthenopteron* (p. 450). In all these respects the lamina superior agrees almost completely in *Rana* and *Eusthenopteron* and it is therefore obvious that it is homologous in the two forms. It is also readily seen that the foremost recurved portion ($pr.\ dim_{rc}$) of the processus dermintermedius of the lateral rostral in *Eusthenopteron* must be the exact equivalent of the antero-medial shank (Smx_{am}) of the septomaxillary in *Rana*. (Equivalents to the posterior horizontal and middle main portions of the processus dermintermedius of the lateral rostral in *Eusthenopteron* are to be found in the other parts of the septomaxillary of Anurans, as will be demonstrated below, p. 535). The ventral one of the two laminae in *Eusthenopteron*, the lamina inferior (p. 443), is formed by the posterior horizontal ($pr.\ im_h$) and middle main portions of the processus intermedius (*pr. im*, figs. 52, 53, 67 A, 70 A, 71 A, 72 A; pp. 442—443). Both in *Eusthenopteron* and in *Rana* the lamina inferior is more strongly developed than the lamina superior and extends backwards as far as the fenestra endonarina anterior (*Eusthenopteron*; *fe. ena*, fig. 67 A) or the fenestra endonarina communis (*Rana*; *fe. en*, fig. 22 A; cf. pp. 513—519 and fig. 67). In both, the lamina as a whole occupies an oblique position, its upper face being directed somewhat dorso-laterally, and throughout its whole length it is continuous laterally with the lamina nariochoanalis (*la. nch*) along (*Eusthenopteron* and several Anurans, pp. 316—317) or slightly below (*Rana*) the dorsal margin of the latter lamina (cf. p. 533). The lamina inferior thus agrees almost completely in *Eusthenopteron* and Anurans and must be homologous in them.

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[1] This slight difference between *Eusthenopteron* and *Rana* is due to the fact that the nasal cavity extends farther forwards in *Rana* (cf. p. 535).

goideus"); *p. tri*, pars triangularis of postnasal wall; *re. vm*, ventro-medial recess of nasal cavity; *ri. lev*, ridge for origin of principal portion of m. levator bulbi; *ri. lh*, lateral horizontal ridge of posterior face of prenasal wall; ri_m, median ridge ascending from floor of cranial cavity; *sn*, septum nasi; *s. olf*, median septum between olfactory canals; *sol. n*, solum nasi; *w. in*, internasal wall; *w. pn*, postnasal wall; *w. prn*, divisio prenasalis communis.

The lamina superior, the lamina inferior and the septomaxillary in *Rana* and their equivalents in *Eusthenopteron* divide the antero-lateral part of the nasal cavity into three compartments, dorsal, middle and ventral. The dorsal and ventral compartments constitute the lateral parts of the recessus superior and recessus inferior, whereas the middle compartment, situated between the other two, is the recessus medius.

Roughly speaking the position of the lateral part of the recessus inferior (*re. i*) is the same in *Rana* (fig. 22 C; p. 313) and *Eusthenopteron* (figs. 52 B, 53, 57 B—D, 69, 71 A, 72 A; pp. 465—466). Its dorsal (dorso-lateral) boundary is likewise similar, in both being formed by the lamina inferior (*la. i*, *Rana*; *pr. im*$_h$, *pr. im*, *Eusthenopteron*). However, the lateral part of the recessus inferior also shows certain differences in the two forms. In *Rana* it is thus provided with an endocranial floor anteriorly, but this is not the case in *Eusthenopteron*, where its foremost portion is floored by dermal bones only (figs. 52 B, 53). In *Rana* there is no canal issuing forwards from it; in *Eusthenopteron* the anterior palatonasal canal (*c*$_a$*p-n*, figs. 52 B, 57 A—C, 58, 71 A) leads forwards between the endocranium and the underlying dermal bones. As we have seen above (p. 477), this canal was probably traversed by the r. palatonasalis (*r. p-n*, figs. 60, 61). The corresponding nerve (see pp. 543—544) in *Rana* (pp. 330—331; *r. pal-n*, figs. 29, 31; cf. *r. p-n*, fig. 71 B, C) runs forwards ventrally to the floor of the foremost portion of the lateral part of the recessus inferior, not until further forward traversing an opening corresponding to the anterior palatonasal canal in *Eusthenopteron* (cf. p. 544). Above (p. 527) it was found that the antero-medial part of the nasal cavity extends further forwards in *Rana* than in *Eusthenopteron*. The differences between *Eusthenopteron* and *Rana* as regards the lateral part of the recessus inferior are clearly due mainly to the fact that this part of the recessus inferior in *Rana* has secondarily widened forwards by a reduction of the prenasal wall. If we assume that the lateral part of the recessus inferior in *Eusthenopteron* developed in a forward direction into the prenasal wall, the new space thus formed would be bounded both by a floor and a lateral wall (figs. 64, 71, 72). The r. palatonasalis (*r. p-n*, fig. 71 B, C) would pass, as in *Rana*, ventrally to the floor of this new space. If then the lateral part of the recessus inferior widened also in a lateral direction in the way shown in figs. 64, 71, and 72, and

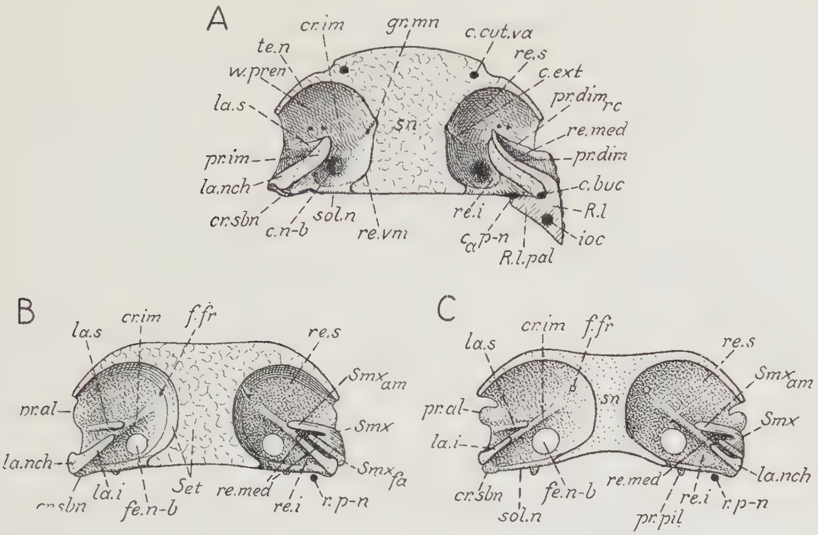

Fig. 71. Three drawings illustrating the probable transformations in the foremost part of ethmoidal region during the development of Anurans from Osteolepiform Crossopterygian ancestors. The posterior parts of the ethmoidal region removed by a transverse section, so that the anterior part of the nasal cavity is shown in posterior aspect. The lateral rostral (septomaxillary) shown on the right side. Sections through cartilage-bone reticulated, through dermal bones ruled. Cartilage dotted. *A*, *Eusthenopteron foordi* Whiteaves. $^2/_1$. *B*, hypothetic primitive Anuran stage. *C*, hypothetic somewhat more advanced Anuran stage. In *B* and *C* the r. palatonasalis shown in transverse section.

R. l, lateral rostral; *R. l. pal*, palatal process of lateral rostral; *Set*, sphenethmoid; *Smx*, septomaxillary; Smx_{am}, antero-medial shank of septomaxillary; Smx_{fa}, external lamina of septomaxillary; $c_a p\text{-}n$, anterior palatonasal canal, transmitting r. palatonasalis; *c. buc*, canal for r. buccalis lateralis; *c. cut. va*, canal for cutaneous vessel; *c. ext*, canal for r. externus narium of n. profundus; *c. n-b*, nasobasal canal; *cr. im*, crista intermedia; *cr. sbn*, crista subnasalis; *fe. n-b*, fenestra nasobasalis, homologous to a middle portion of nasobasal canal in *Osteolepiformes*; *f. fr*, foramen frontale, transmitting r. externus narium and corresponding to the canal *c. ext* in *Osteolepiformes*; *gr. mn*, groove for r. medialis narium of n. profundus; *ioc*, infraorbital sensory canal; *la. i*, lamina inferior; *la. nch*, lamina nariochoanalis; *la. s*, lamina superior; *pr. al*, processus alaris; *pr. dim*, processus dermintermedius of lateral rostral; $pr.\ dim_{rc}$, antero-medio-dorsal recurved portion of processus dermintermedius; *pr. im*, processus intermedius (middle main portion) of lamina nariochoanalis (lamina inferior); *pr. pil*, processus prenasalis inferior lateralis; *re. i*, *re. med*, *re. s*, recessus inferior, recessus medius and recessus superior of nasal cavity; *re. vm*, ventro-medial recess of nasal cavity; *r. p-n*, r. palatonasalis; *sn*, septum nasi; *sol. n*, solum nasi; *te. n*, tectum nasi; *w. pren*, prenasal wall (lateral part of divisio prenasalis communis).

in addition the parts of the dermal skeleton situated underneath it (the hinder part of the ridge-like connection made up of the antero-lateral process of the vomer and the adjacent part of the pars palatina of the naso-rostro-premaxillary; cf. p. 450) were reduced, a space would obviously arise which in all respects would be as the lateral part of the recessus inferior in *Rana*. In consequence of the said reductions of the dermal bones the hinder part of the anterior palatonasal canal would disappear. If the reduction of the antero-lateral process (*pr. Vo*, fig. 64 A) of the vomer and of the lateral process (*pr*$_l$*NRP*$_3$) of the pars palatina of the naso-rostro-premaxillary proceeded so far that only a short anterior part of each of them persisted, the anterior palatonasal canal would be represented by an opening bounded by the endocranium dorsally and by the remainder of the antero-lateral process of the vomer (*pr. Vo*, fig. 64 B) and the lateral process (*pr*$_l$*Pmx*$_3$) of the pars palatina of the "premaxillary" ventrally. This opening would thus agree with the one in *Rana* that has been interpreted (p. 544) as representing the anterior palatonasal canal in *Eusthenopteron.*

The recessus medius in *Rana* (*re. med*, figs. 22 A, C, 69; p. 313) is bounded anteriorly by the prenasal wall and ventrally by the lamina inferior. Its dorsal boundary is formed anteriorly by the lamina superior and posteriorly and postero-laterally to this lamina by the septomaxillary (*Smx*, fig. 29). This bone is horseshoe-shaped and through the opening between its antero-medial and postero-lateral shanks the recessus medius is in communication with the recessus superior. The recessus medius in *Eusthenopteron* (*re. med*, figs. 52 B, 57 A—D, 58 B, 71 A, 72 A; p. 465), which is very small, lies mainly dorsally to the processus dermintermedius of the lateral rostral, and is bounded both ventrally and anteriorly by the foremost part of the middle main portion of the process. However, the antero-medio-dorsal recurved portion of the processus dermintermedius (*pr. dim*$_{rc}$) is developed so as to form a roof of the recess and probably corresponds to the antero-medial shank of the septomaxillary (*Smx*$_{am}$) in *Rana* (see p. 529). As is demonstrated by figs. 29 and 69 (cf. fig. 72 C) this shank of the septomaxillary forms the roof only of a small middle part of the recessus medius in *Rana.* The recessus medius in *Eusthenopteron*, which is entirely situated below the antero-medio-dorsal recurved portion of the processus dermintermedius, thus corresponds only to a small middle part of the recessus medius in *Rana*, i. e. only to the part situated just below the antero-medial shank of the septomaxillary. The recessus medius of *Rana* has thus a considerably larger extent both forwards and backwards than that of *Eusthenopteron* (cf. fig. 72 A, C), and to a large extent it lies deeper down in the skeleton. Its hinder part even extends backwards underneath the postero-lateral shank of the septomaxillary (*Smx*, fig. 69; cf. *Smx*$_{pl}$, figs. 68 C, 70 C). This latter part of the septomaxillary is situated postero-laterally to and at a somewhat lower level than the antero-medial shank, exactly as are the posterior horizontal and middle main portions of the processus dermintermedius in *Eusthenopteron* in relation to the antero-medio-dorsal recurved portion, and it is therefore obviously homologous to them. The equivalents of the posterior deeper parts of the recessus medius in *Rana* are thus to be sought in *Eusthenopteron* ventrally to the two posterior portions of the processus dermintermedius, between that process and the processus intermedius, but here these two processes rest tightly against one another (figs. 53, 71 A) and there is no space whatever between them. Such a space may, however, have arisen in the following way (figs. 67, 68, 70—72). The small recessus medius in a form like *Eusthenopteron* was first somewhat widened in antero-ventral direction by the reduction of a short anterior medial part of the middle main portion of the processus dermintermedius just below its antero-medio-dorsal recurved portion (*pr. dim*$_{rc}$). In this way a narrow but deep transverse incisure was formed in the anterior part of the medial margin of the processus dermintermedius (figs. 68 B, C, 70 B, C, 71 B, C). After this the recessus medius continued to widen both forwards, at the cost of the foremost part of the processus intermedius and the adjacent part of the prenasal wall, and backwards between the processus dermintermedius and the processus intermedius through a reduction of the upper superficial parts of the latter process (fig. 72). The recess would now include both a homologue of the primary small recessus medius in *Eusthenopteron* and a new space. This new space would on the whole be situated deeper down than the primary recess and would also extend further forwards and backwards. It would be bounded laterally by a raised margin formed by the lamina nariochoanalis and ventromedially by the thin middle main and posterior horizontal portions of the processus intermedius, which, as we have already seen, together correspond to the lamina inferior of the frog. The new space would be roofed posteriorly by the posterior horizontal and middle main portions of the processus dermintermedius and anteriorly by the lamina superior, and it would be in communication dorsally with the primary recessus medius and the recessus superior through the incisure in the medial margin of the processus dermintermedius. Regarded as a whole the recess would now agree exactly with the recessus medius in *Rana*. The deep incisure in the medial margin of the processus dermintermedius of the lateral rostral would make this process (figs. 68 B, C, 70 B, C, 71 B, C, 72 B, C) fundamentally horseshoe-shaped, like the septomaxillary in *Rana* (figs. 29, 69), with an antero-medial shank (*Smx*$_{am}$) lying along the postero-lateral margin of the lamina superior and a postero-lateral shank (*Smx*$_{pl}$) bounding the posterior part of the recessus medius from above. The two shanks would also be connected with one another anterolaterally, in a similar way as in *Rana*.

The lateral part of the recessus superior in *Eusthenopteron* (*re. s*, figs. 52 B, 53, 57 A, C, D, 71 A, 72 A; pp. 464—465) agrees fundamentally with the corresponding part of the recessus superior in *Rana* (*re. s*, figs. 22 C, 69; cf. figs. 22 A, E, 29; p. 313). It thus lies medially to the fenestra endonarina anterior, which is about as long as the fenestra endonarina communis in *Rana* (cf. fig. 67). Its foremost portion is bounded ventrally by the lamina superior and the antero-medio-dorsal recurved portion of the processus dermintermedius, which correspond to the lamina superior and the antero-medial shank of the septomaxillary in Anurans. Its hinder and larger portion is bounded ventrally by the middle main and posterior horizontal portions of the processus dermintermedius, which are the equivalents of the postero-lateral shank of the septomaxillary in Anurans. The lamina superior and the recurved portion of the processus dermintermedius, like the corresponding formations in *Rana*, are situated higher up than the other parts of the ventral boundary, and the foremost portion of the lateral part of the recess is thus in both considerably lower than its posterior portion. The lateral part of the recessus superior in *Eusthenopteron* differs from that in *Rana* only by its not extending so far forwards in the prenasal wall. It is obvious, however, that also in this respect it would be exactly as that in *Rana* if it developed slightly in an anterior direction through a reduction of the part of the divisio prenasalis communis (prenasal wall) in front of it (figs. 67, 70—72). Its foremost portion would then form a space bounded dorsally and laterally by endoskeletal walls and, if the recessus medius developed as assumed above (p. 533), ventrally by a rather extensive lamina superior. Anteriorly it would be separated from the cavum prenasale, created by reductions in the anterior parts of the divisio prenasalis communis (pp. 502—503), by a thin prenasal wall only. A partial reduction of the dorsal and ventral parts of its lateral wall would then result in the development of a processus alaris (*pr. al*, figs. 67 B, C, 70 B, C, 71 B, C; cf. p. 519) similar to that of the frog.

As may be gathered from the above, the anterior and antero-lateral parts of the nasal cavity in *Eusthenopteron* are developed fundamentally as the corresponding ones in *Rana*, differing from these only in that they are simpler and more primitive. These parts of the nasal cavity in *Eusthenopteron* are thus decidedly of a primitive Anuran type. By mostly quite inconsiderable modifications, above all widenings in connection with reductions of the endoskeleton and the lateral rostral, they would become exactly as in Anurans. Through such widenings the various crests and laminae in the anterior and antero-lateral parts of the nasal cavity in *Eusthenopteron* would also become very much as in Anurans. The crista intermedia, the lamina superior and the middle main portion of the processus intermedius would increase in forward extent. The processus intermedius would be thinner and would enter into the ventral boundary of the recessus medius; its main and posterior portions would together form a lamina inferior. The processus dermintermedius would be transformed into a septomaxillary. The nasal septum would be narrower and the lateral part of the divisio prenasalis communis would be only a thin prenasal wall separating the nasal cavity from the cavum prenasale. Finally, the canalis nasobasalis would be transformed into a mere foramen.

That the nasal cavity has actually extended forwards in the Anurans is supported by the fact that such an extension takes place during the embryonic development in *Rana* (GAUPP 1893, p. 422). It is of interest in this connection that towards the end of the metamorphosis the ethmoidal region in *Calyptocephalus* becomes "zierlicher" and the lamina superior increases in rostro-caudal extent (REINBACH 1939, pp. 262, 264).

We may now be justified in drawing the following conclusions. The crista intermedia and the lamina superior in *Eusthenopteron* are true homologues of the similarly termed formations in Anurans. The middle main and posterior horizontal portions of the processus intermedius in *Eusthenopteron* together correspond to the lamina inferior in Anurans and may therefore be referred to under the common term of lamina inferior. The lamina nariochoanalis in *Eusthenopteron* constitutes an anterior ventral part of the lateral nasal wall but does not include any part of the solum nasi and must therefore be homologous to the lamina nariochoanalis in Anurans. The processus dermintermedius in *Eusthenopteron* is the homologue of the septomaxillary in Anurans; the latter bone is thus a vestige of the lateral rostral of the *Osteolepiformes*. The antero-medio-dorsal recurved portion of the processus dermintermedius corresponds to the antero-medial shank of the septomaxillary, whereas the middle main and the posterior horizontal portions of the processus dermintermedius are in the main equivalent to the postero-lateral shank of the septomaxillary. The incisure or gap in the medial margin of the septomaxillary in Anurans is a secondary formation caused by the widening of the recessus medius. The recessus superior, the recessus medius and the recessus inferior in *Eusthenopteron* are true homologues of the similarly termed recesses in Anurans, and differ from those only in their smaller extent.

The hinder part of the nasal cavity in *Eusthenopteron* (figs. 47, 48, 51, 57, 70 A; pp. 464—466) is of a simple construction similar to that in *Rana* (figs. 22 A, D, 27 B; p. 313). Its walls are however much more complete in *Eusthenopteron* than in *Rana*, due to reductions in the latter form (cf. pp. 512—519). In *Eusthenopteron* there are two recesses, the recessus ventro-medialis and the recessus lateralis. The recessus ventro-medialis (*re. vm*, figs. 52 A, 57 B, D, 70 A, 71 A; p. 466) lies ventro-medially to the main chamber of the nasal cavity and must have housed a ventro-medial bulge of the nasal sac (*di. vm*, fig. 59), no doubt corresponding to the diverticulum mediale or Jacobson's organ (*di. m*, figs. 27 A, 28; pp. 324—325) in Anurans. This organ was thus in all probability developed even in *Eusthenopteron* where it lay almost exactly as in *Rana* (cf. p. 326). No recessus ventro-medialis is developed in Anurans, but this is certainly due to the narrowing of the nasal septum (cf. p. 527). The recessus lateralis in *Eusthenopteron* (*re. l*, figs. 51, 57; p. 466) as in *Rana* (p. 315, fig. 27 B) lies laterally to the postero-ventral part of the main chamber of the nasal cavity and dorso-laterally to the fenestra endochoanalis. In both it is continuous anteriorly with the recessus inferior, medially with the main chamber of the nasal cavity, whereas posteriorly it communicates with the mouth cavity. It is bounded laterally and ventrally by the postero-ventral medially curved part — *w. lic* (figs. 47 B, C, 48, 51) in *Eusthenopteron;* the anterior part of the pars triangularis (*p. tri*) and the processus maxillaris anterior (*pr. mxa*, fig. 22 A, D; cf. fig. 67 B, C) in *Rana* (cf. C. A. Du Toit 1933, fig. 2 a, b; De Villiers 1934 a, p. 298, fig. 3) — of the lateral nasal wall but has no definitive dorsal boundary. The lateral recess has thus on the whole the same position and boundaries in *Eusthenopteron* and *Rana* and it is undoubtedly homologous in the two forms.

The lateral recess in Anurans houses the diverticulum laterale (*di. l*) of the nasal sac (figs. 27 A, 28; p. 325) and obviously the lateral recess in *Eusthenopteron* must have been developed for a corresponding diverticle. There was thus certainly a diverticulum laterale in *Eusthenopteron* (*di. l*, fig. 59; p. 467). As in Anurans, this diverticle opened ventro-medially into the choana. Judging from the connection between the lateral recess and the mouth cavity, the cavity of the diverticle, the sinus lateralis nasi, as in Anurans, communicated posteriorly with the mouth cavity through a sulcus maxillo-palatinus (*sulc. mx-pal*, fig. 27 B) bounded ventrally by a plica palatina (*pl. pal*). The postero-ventro-lateral part of the nasal cavity in *Eusthenopteron* lies, as a whole, lower than the other ventral parts of the nasal cavity and is somewhat produced in a caudal direction (fig. 57 A, B, E; p. 464). This obviously implies that the diverticulum laterale had a more ventral position than the other parts of the nasal sac and extended further backwards than the postero-medial parts of the nasal sac. Also in these respects we find a striking agreement between *Eusthenopteron* and *Rana* (see figs. 27 B, 28 A; cf. also Nemours 1930, fig. 16; Rowedder 1937, fig. 12).

Since, as demonstrated above, the nasal cavity in *Eusthenopteron* is fundamentally of a primitive Anuran type, the nasal sac in *Eusthenopteron* must clearly also otherwise have been in the main as in Anurans. The nasal sac was thus in *Eusthenopteron* at least to some extent subdivided into divisions corresponding to those in *Rana* (pp. 322—325; figs. 27, 28 A; cf. figs. 28 B, 72 B, C) and probably consisted of the following divisions (figs. 59, 72 A; pp. 466—467): A large diverticulum principale from which the choanal tube issued in a ventral direction and with a vestibular portion (*vest*) in the postero-lateral part of the recessus superior medially to the fenestra exonarina anterior; a saccus superior (*di. s*) which occupied the anterior parts of the recessus superior and was continuous with the diverticulum principale; a diverticulum inferius (*di. i*) which occupied the recessus inferior and formed a diverticulum mediale (Jacobson's organ; cf. p. 536); a diverticulum laterale with a sinus lateralis continuous with the mouth cavity by a sulcus maxillo-palatinus; and finally a small diverticulum medium (*di. med*) which was an anterior bulge of the vestibular portion of the diverticulum principale, below the lateral part of the saccus superior, and lay in the recessus medius.

Both the anterior external nasal tube and the nasolachrymal duct (*dnl*, fig. 72 A; posterior external nasal tube, *ntp*, fig. 59) were in *Eusthenopteron* given off from the vestibular portion (*vest*) of the diverticulum principale, and the nasolachrymal duct passed backwards dorsally to the posterior portions of the processus dermintermedius corresponding to the postero-lateral shank of the septomaxillary in Anurans. In *Rana* (figs. 27, 28 A; cf. figs. 28 B, 72 C) the diverticulum medium is comparatively large and continuous with the vestibular portion through a narrow duct-like portion which forms part of the tuba infundibuli (*t. inf*). The diverticulum medium lies ventrally to the lamina superior and the septomaxillary, between these and the lamina inferior, but its duct-like portion passes upwards through the opening between the shanks of the septomaxillary. Only the anterior external nasal tube issues from the vestibular portion whereas the nasolachrymal duct goes off backwards from the postero-lateral corner of the diverticulum medium. It is readily seen that these differences between the nasal sac in *Eusthenopteron* and *Rana* are on the whole correlative with the different development of the recessus medius (pp. 532—533) in the two forms, and chiefly due to a secondary increase in size of the diverticulum medium in *Rana* and Anurans in general. This increase in size has also affected the vestibular portion of the diverticulum principale in such a way that the nasolachrymal duct issues lower down. The place of origin of the duct from the nasal sac has moved downwards and has become incorporated in the diverticulum medium. It is also obvious that the saccus superior and the diverticulum inferius in Anurans developed progressively in an anterior direction in Anurans. The main differences as regards the nasal sac in

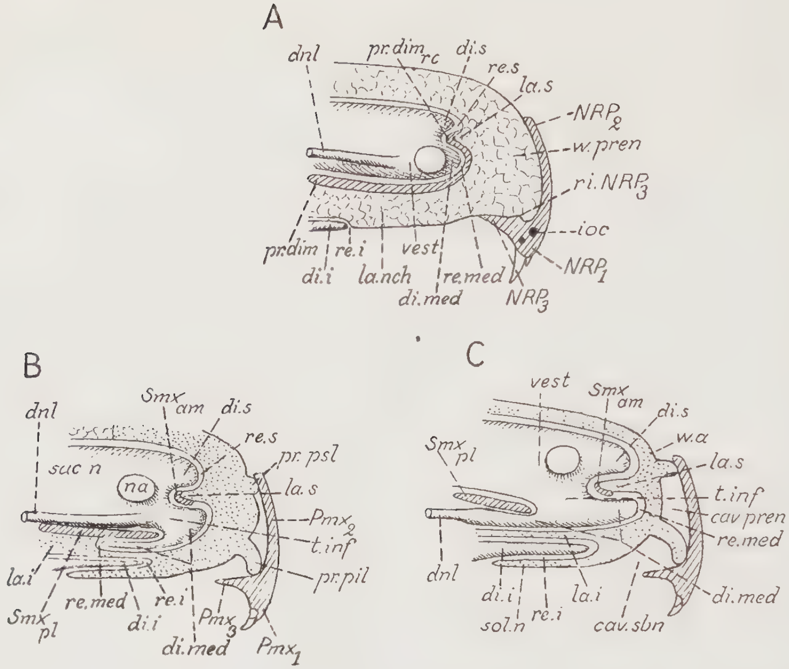
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Fig. 72. Three drawings illustrating probable changes in the anterior parts of the skeleton of the snout, in the anterior parts of the nasal cavity, and in the anterior parts of the nasal sac during the development of Anurans from primitive Osteolepiform Crossopterygian ancestors. Skeleton shown in sagittal section. Anterior parts of nasal sac diagrammatically restored. Cross-sections through cartilage-bone reticulated, through dermal bones ruled. Cartilage dotted. *A*, *Eusthenopteron foordi* Whiteaves. *B*, hypothetic primitive Anuran stage. *C*, hypothetic somewhat more advanced Anuran stage.

NRP_1, NRP_2, NRP_3, pars dentalis, pars facialis, and pars palatina of naso-rostro-premaxillary; Pmx_1, Pmx_2, Pmx_3, pars dentalis, pars facialis, and pars palatina of Anuran "premaxillary", homologous to the naso-rostro-premaxillary in *Eusthenopteron*; Smx_{am}, Smx_{pl}, antero-medial and postero-lateral shanks of septomaxillary; *cav. pren*, cavum prenasale; *cav. sbn*, cavum subnasale; *di. i*, *di. med*, diverticulum inferius and diverticulum medium of nasal sac; *di. s*, saccus superior of nasal sac; *dnl*, ductus nasolacrimalis; *ioc*, infraorbital sensory canal; *la. i*, lamina inferior; *la. nch*, processus intermedius of lamina nariochoanalis; *la. s*, lamina superior; *na*, anterior external nostril; *pr. dim*, processus dermintermedius of lateral rostral; $pr.\ dim_{rc}$, antero-medio-dorsal recurved portion of processus dermintermedius *pr. pil*, processus prenasalis inferior lateralis; *pr. psl*, processus prenasalis superior lateralis; *re. i*, *re. med*, *re. s*, recessus inferior, recessus medius and recessus superior of nasal cavity; $ri.\ NRP_3$, ridge on dorsal face of pars palatina of naso-rostro-premaxillary; *sac n*, nasal sac; *sol. n*, solum nasi; *t. inf*, tuba infundibuli; *vest*, vestibular portion of diverticulum principale; *w. a*, prenasal wall; *w. pren*, divisio prenasalis communis (prenasal wall .

Eusthenopteron and Anurans are thus on the whole due to a progressive development in the latter forms as demonstrated in fig. 72.

The above conclusions concerning the progressive development of the various divisions of the nasal sac and the shifting downwards of the nasolachrymal duct and its place of origin from the nasal sac are corroborated by the following conditions in Anurans.

1) The nasolachrymal duct in larvae of *Calyptocephalus* first lies dorsally to the septomaxillary (p. 318). It then migrates downwards through the septomaxillary, so that in the adults it lies ventrally to that bone, as in other Anurans (cf. No. 4, p. 514).

2) In *Ascaphus*, which is generally regarded as one of the most primitive recent Anurans, the diverticulum medium is small and the nasolachrymal duct does not issue from the diverticulum medium itself, but somewhat higher up, from the transition between the tuba infundibuli and the diverticulum medium (pp. 326—327; cf. fig. 72 B).

3) The diverticulum medium in larvae of Anurans (*Alytes*, *Bufo*, *Pelobates*; Rowedder 1937, p. 115, figs. 5, 9, 18) arises at the beginning of the metamorphosis as an anterior horizontal bulge from the vestibular portion of the nasal sac. This bulge lies between the saccus superior ("orale Kuppel", Rowedder) and the diverticulum inferius. The diverticulum medium in *Eusthenopteron* (p. 467; *di.med*, fig. 72 A; cf. *re.med*, fig. 57 A—D) must obviously have been a similar bulge from the vestibular portion of the nasal sac and lay also between the saccus superior and the diverticulum inferius. Quite as in the larvae of Anurans, it had a somewhat oblique position, so that its lateral part was situated slightly in front of its medial part.

In *Rana* are found two nasal muscles, both of which are developed in relation to the external nostril (Bruner 1901, pl. 17, fig. 8; Ecker-Wiedersheim-Gaupp 1904, p. 671). One of these muscles, the m. lateralis narium (*m.ln*, fig. 27 A), arises from the anterior (upper) parts of the lamina obliqua, the other, the m. medialis narium, from the ventral part of the anterior margin of the pars terminalis and from the adjacent part of the postero-lateral shank of the septomaxillary. Muscles corresponding to these two in the frog may have been present also in *Eusthenopteron*. As may be gathered from fig. 67, the homologue of the anterior parts of the lamina obliqua in Anurans is to be sought for in *Eusthenopteron* in the portion of the lateral nasal wall that lies above the anterior parts of the fenestra endonarina anterior. Just below that portion of the lateral nasal wall in *Eusthenopteron* we find, on the medial face of the anterior tectal, a small shallow depression or recess (*re.m.ln*, figs. 52 B, 57 A, C, D; p. 449), which may have served as a place of origin of a muscle corresponding to the m. lateralis narium of the frog. Another small recess in *Eusthenopteron* (*re.m.mn*, figs. 52 B, 57 A—C, 58 A; p. 449) lies immediately postero-medially to the posterior corner of the fenestra exonarina anterior, just above the posterior portion of the processus dermintermedius, which, as we have seen above, corresponds to the hinder part of the postero-lateral shank of the septomaxillary in Anurans and covers the part of the processus intermedius (lamina inferior) that presumably forms the ventral part of the pars terminalis in Anurans (see foot-note 1 on p. 518). This small recess may thus very well be the place of origin of a muscle corresponding to the m. medialis narium of the frog.

The shape of the foremost part of the cranial cavity indicates that the anterior part of the brain in *Eusthenopteron* (pp. 462—464; fig. 59) was fundamentally as in *Rana* (pp. 327—328; fig. 30). The forebrain was thus of approximately the same breadth as the diencephalon (cf. p. 395). The hemispheres (*hem*) were elongate, lay close to one another, and were separated by a dorsal and a ventral median groove only or possibly by a narrow fissura sagittalis (*fiss*). The bulbi olfactorii (*b. olf*) were situated close to one another immediately in front of the hemispheres. Though they do not seem to have been bounded off from one another on the dorsal side, they were separated by a median groove on the ventral side. The olfactory nerves (*I*) were also approximately as in *Rana*.

The canals and various passages of the snout in *Eusthenopteron* could be followed practically throughout their extent and their relations to the skeleton could be established in detail. If the majority of them are assumed to have housed nerves, the nervous system of the snout in *Eusthenopteron* as thus restored differs considerably from that in other fishes and Urodeles, whereas both in its general features and as to details it agrees, as we shall now see, almost completely with that in *Rana*. In these circumstances we are justified in concluding that the nerves and nerve-branches of the snout in *Osteolepiformes* were strictly homologous to the similarly termed ones in Anurans.

During its passage through the orbit the n. profundus (*n. pr*) in *Eusthenopteron* gave off at least one lateral and one medial dorsal branch. The lateral branch, the r. frontalis anterior (*r. fra*, figs. 59, 61; p. 476), left the orbit through the canal *c. fra* (figs. 47, 49, 50; p. 471) and emerged on the dorsal face of the ethmoidal region. Judging from the position and direction of the canal the branch in question issued from the n. profundus fairly far back in the orbit and went forwards to the area of the snout behind the fenestra exonarina anterior. It seems to have resembled and may be regarded as a homologue of the anterior one of the dorsal profundus branches in *Rana* called the rr. frontales et palpebrales superiores anteriores (*rr. fra*, fig. 30; p. 328). The medial dorsal branch, the r. frontalis perforans (*r. perf.* figs. 59, 61; p. 476), ascended to the dorsal face of the ethmoidal region through the canal *c. perf* (figs. 47, 49, 50; p. 471), issued from the n. profundus fairly close behind the postnasal wall and supplied a dorso-medial area on the upper side of the snout. It appears to have corresponded to the r.

frontalis perforans in *Rana* (figs. 29, 30; p. 328), but was given off from the n. profundus further caudally than that branch. The canal *c. perf* in *Eusthenopteron* is then homologous to the canal for the r. frontalis perforans in *Rana* (cf. p. 328, figs. 29, 30, and *c. perf*, fig. 67).

The n. profundus in *Eusthenopteron* left the orbit through the profundus canal (*c. pr*, figs. 48—51, 57 A—C, E, 59; p. 470) in which, quite as in *Rana* (p. 328; cf. fig. 30) it bifurcated into a lateral and a medial nasal branch, both of which entered the nasal cavity. The lateral nasal branch, the r. lateralis narium (*r. ln*, figs. 59, 61; p. 476) went dorsally to the nasal sac towards the fenestra endonarina anterior. In most respects it was probably developed as the r. lateralis narium in *Rana* (figs. 29, 30; p. 328) with which it was certainly homologous. The medial nasal branch, the r. medialis narium (*r. mn*, figs. 59, 61; pp. 476—477), first ran forwards and medially dorsally to both the olfactory nerve and the nasal sac until it reached the medial nasal wall (the septum nasi) on the lateral face of which it went forwards and downwards in a marked groove (*gr. mn*, figs. 47 B, 57 A, D; pp. 439, 470). From this groove it descended into the medial part of the recessus inferior at the anterior end of which it left the nasal cavity through the nasobasal canal (*c. n-b*, figs. 52, 57 A—C; p. 470). At its entrance into the recessus inferior just behind the medial end of the crista intermedia (*cr. im*) it gave off a fine dorso-medial twig, the r. externus narium (*r. ext*), which ascended to the dorsal side of the ethmoidal region through the canal *c. ext* (figs. 47, 57 B—D; p. 470). It did not send out any other twig in the nasal cavity to the dorsal side of the ethmoidal region and was therefore in this respect very different from the corresponding nerve in *Porolepiformes* and Urodeles (cf. pp. 303, 378, 394; figs. 21, 43). Having thus traversed the nasal cavity without giving off more than one dorsal branch it was still a strong nerve at its entrance into the nasobasal canal. Within that canal it sent first a strong ventral branch ($r_v mn$, figs. 59—61 to the prenasal pit and the fossa apicalis through the ventral branch of the nasobasal canal ($c_v n\text{-}b$, figs. 48, 56, 57 B—D). Somewhat further forwards it bifurcated into a medial ($r_m ap$) and a lateral ($r_l ap$) terminal branch, which after leaving their respective branches of the nasobasal canal ($c_m n\text{-}b$, $c_l n\text{-}b$) broke up into numerous twigs, the rr. apicales (*rr. ap*), which entered the naso-rostro-premaxillary through the two groups of small foramina ($f.\,ap_l$, $f.\,ap_m$, fig. 68 D) on the posterior face of the pars facialis. Both the course and the mode of branching of the r. medialis narium were exactly as in *Rana* (figs. 29, 30; pp. 328—329) and every one of its branches has an exact equivalent in that form. Within the nasal cavity the r. medialis narium in *Rana* (*r. mn*) thus gives off a single branch only. This branch, the r. externus narium (*r. ext*), issues immediately behind the medial end of the crista intermedia, leaves the nasal cavity through the foramen frontale and goes forwards and upwards. Its agreement with the similarly termed twig in *Eusthenopteron* shows not only that the two nerve branches must be strictly homologous, but also that the foramen frontale in *Rana* must correspond exactly to the canal *c. ext* in *Eusthenopteron* (cf. p. 527). During its passage through the fenestra nasobasalis the r. medialis narium in *Rana* gives off a ventral branch ($r_v mn$) corresponding to the similarly situated ventral branch in *Eusthenopteron* and then bifurcates into two terminal branches, one medial ($r_m ap$) and one lateral ($r_l ap$), corresponding to the medial and lateral terminal branches in *Eusthenopteron*. Each of these two terminal branches breaks up into numerous small twigs, the rr. apicales (*rr. ap*), which go to the very tip of the snout as in *Eusthenopteron*. From the course and development of the prenasal parts of the r. medialis narium it is readily seen that the fenestra nasobasalis in *Rana* corresponds to a hinder part of the nasobasal canal in *Eusthenopteron* (cf. pp. 503, 527).

The r. maxillaris V in *Eusthenopteron* (*r. mx*, fig. 61; pp. 477—479) gave off a branch far back in the orbit which in all probability anastomosed with the r. palatinus VII. This branch, the postchoanal anastomosis (*ast. pch*, figs. 60, 61), first went forwards in the vento-lateral part of the orbit and was then enclosed in a canal, *c. ast* (p. 472), in the uppermost parts of the dermopalatine. After leaving that canal it took an antero-medial course through the foremost part of the orbit, crossing the dermopalatine in the groove $gr_1 ast$ (fig. 54 B) postero-medially to the anterior end of the bone and antero-laterally to the articulation between the lateral ethmoidal articular area ($art_2 l$, fig. 54) of the palatoquadrate and the lateral autopalatine articular area ($art_1 l$, figs. 48—50) of the ethmoidal region. Through the notch *i. ast* (figs. 54 B, 56) in the medial margin of the dermopalatine it went downwards to the lower side of the dermopalatine, that is to say to the mouth cavity, where it continued a short distance posteriorly and medially before it passed over into the r. palatinus VII. The postchoanal anastomosis in the adult *Rana* (figs. 29—31; p. 330) is in several respects much as that in *Eusthenopteron*. It is thus given off from the r. maxillaris V far posteriorly in the orbit, then goes forwards in the lateral part of the orbit, and curves downwards to the mouth cavity postero-medially to the anterior end of the dermopalatine. A considerable difference from the conditions in *Eusthenopteron* is, however, that it leaves the orbit through the antero-lateral corner of the fenestra subocularis (*fe. sboc*, fig. 22 A) and thus goes down to the mouth cavity postero-medially to the connection between the palatoquadrate bar and the postnasal wall. In larval stages of Anurans (pp. 332—333), however, the postchoanal anastomosis passes down to the mouth laterally to the connection between the palatoquadrate (processus quadrato-ethmoidalis) and the ventro-lateral corner of the postnasal wall (processus maxillaris posterior), quite as in *Eusthenopteron*, and not until the end of the metamorphosis does it acquire its definitive position by "migrating" in a medial direction through the palatoquadrate (cf. pp. 522—523).

From the postchoanal anastomosis in *Eusthenopteron* a branch (*r. vot*, figs. 60, 61; p. 477) was probably given off to the tusks and conceivably also to the other teeth of the vomer. Since, as far as I can find, nothing is known concerning the innervation of the vomeral teeth in *Rana* or other Anurans, it is impossible to say at present whether there is any branch from the postchoanal anastomosis in Anurans equivalent to the one in *Eusthenopteron* just referred to.

The supposed r. palatonasalis in *Eusthenopteron* (*r.p-n*, figs. 60, 61; pp. 477—478) must have branched off from the main trunk of the r. maxillaris somewhere in the middle part of the orbit. It passed forwards in the posterior palatonasal canal ($c_{p}p$-n, $gr_{p}p$-n, figs. 54, 65 A) laterally to or partly in the dermopalatine and then traversed the opening *f. buc* (fig. 55) laterally to the lateral articular connection between the pars autopalatina of the palatoquadrate and the postnasal wall and thus ventro-laterally to the processus postero-ventralis (*pr. pv*; figs. 47 B, 48, 55, 65 A) at the ventro-lateral corner of the postnasal wall. From here it continued forwards laterally to the choana, presumably in the mucous membrane covering the ventro-lateral face of the ventral medially curved part (*w. lic*, figs. 47 B, C, 48, 56) of the lateral nasal wall. It then traversed the anterior palatonasal canal ($c_{a}p$-n, figs. 52 B, 56, 57, 58; cf. *gr. p-n*, fig. 48) and emerged into the prenasal pit. The r. palatonasalis in the adult *Rana* (*r. pal-n*, figs. 29, 31; pp. 330—331) accompanies the postchoanal anastomosis through the anterior ventro-lateral part of the orbit and through the fenestra subocularis. It then goes forwards ventrally and medially to the connection between the palatoquadrate and the ventro-lateral corner of the postnasal wall and ventrally to the dermopalatine. In larval stages the nerve has the same relations to the postnasal wall and the foremost part of the palatoquadrate as the supposed r. palatonasalis in *Eusthenopteron*, but it then "migrates" in a medial direction and in adults ultimately traverses the fenestra subocularis (pp. 332—333). The embryonic development thus shows that the difference in the course of the r. palatonasalis in *Eusthenopteron* and the adult *Rana* must be due to a secondary modification in the latter form. That the r. palatonasalis in *Eusthenopteron* passed laterally to or laterally to and partly within the dermopalatine but in *Rana* goes ventrally to the dermopalatine is certainly due to the weak development of that bone in *Rana* (cf. p. 550 and figs. 64, 65). In the ethmoidal region the r. palatonasalis in *Rana* runs first laterally to the choana and ventrally to the antero-lateral part of the nasal sac, quite as it seems to have done in *Eusthenopteron*. Further anteriorly in *Rana* it goes ventrally to the part of the solum nasi that constitutes the ventral boundary of the recessus inferior of the nasal cavity (cf. *r.p-n*, fig. 71 B, C and p. 530) and gives off a medial branch, which together with the antero-lateral terminal branch ($r_{al}pal$) of the r. palatinus VII forms the prechoanal anastomosis (*ast. prech*). As illustrated by fig. 31, it then continues forwards dorsally to the apex of the antero-lateral process of the vomer (cf. p. 499; cf. also fig. 64 B, *pr. Vo*). In certain specimens this process extended so far antero-laterally as to meet the lateral process of the pars palatina of the "premaxillary" (p. 499; pr_lPmx_3, fig. 23 B; cf. fig. 64 B) and in these cases the r. palatonasalis traverses a narrow opening bounded ventrally by the antero-lateral process of the vomer and the pars palatina of the "premaxillary" and dorsally by the ventral face of the endocranium. This opening obviously corresponds to the anterior palatonasal canal in *Eusthenopteron* (cf. pp. 530—532). That it is very short and only fortuitously present is due simply to the fact that both the ethmoidal region and its dermal bones are much more weakly and imperfectly developed in *Rana* than in *Eusthenopteron*.

The r. palatonasalis in *Rana* (*r. pal-n*, figs. 29, 31) gives off several lateral branches, which, judging from their course, were probably distributed to the teeth of the maxillary and "premaxillary", though this could not be confirmed. In *Eusthenopteron* the teeth of the naso-rostro-premaxillary and at least also those of the anterior part of the maxillary were supplied by nerves (*rr. Mx + Pmx*, figs. 60, 61; p. 478) which conceivably were branches of the r. palatonasalis.

Besides the r. palatonasalis *Rana* possesses another maxillaris branch to the snout, the r. infraorbitalis (*r. io*, figs. 29, 30; p. 330). This nerve passes forwards in the skin outside both the lateral part of the postnasal wall and the "nasal" bone. Outside the "nasal" it accompanies the nasolachrymal duct (*dnl*). It is quite likely that this branch was present also in *Eusthenopteron* (*r. io*, figs. 59—61; p. 477), where it must be assumed to have left the orbit through the wide foramen *fe. enp* in the postnasal wall, which most probably is the fenestra endonarina posterior (cf. pp. 446—447, 513) through which the nasolachrymal duct emerged from the nasal cavity into the foremost lateral part of the orbit. That it passed medially both to the lateral nasal wall and to the external dermal bones does not prevent its homology to the r. infraorbitalis in *Rana* (cf. p. 514). If actually present in *Eusthenopteron*, the nerve in question must thus have accompanied the nasolachrymal duct (posterior external nasal tube) forwards to the vicinity of the fenestra endonarina anterior. Here, like its homologue in *Rana*, it may have anastomosed with a branch of the r. lateralis narium of the n. profundus.

The rr. cutanei maxillares in *Eusthenopteron* (*rr. cut*, fig. 61; pp. 478—479) which passed both backward and forward, entering and piercing the dermal bones constituting the ventro-lateral boundary of the orbit, undoubtedly correspond to the rr. cutanei maxillares in *Rana* (figs. 29, 30; p. 330), which go in similar directions and are distributed to the skin outside the maxillary.

As we have seen above (pp. 470—471), two fine canals, *c. n. va* (figs. 52 A, C, 57 A—D), lead in *Eusthenopteron* from the recessus superior forwards into the prenasal wall. Judging from their position and direction these two canals may have given passage to twigs either of the r. infraorbitalis or of the r. lateralis narium of the n. profundus. Besides the nerves they may also have transmitted vessels. It is not known whether any corresponding prenasal nerve-twigs exist in *Rana*. In *Calyptocephalus* Reinbach (1939, pp. 259, 261, 265) has described certain fine nerve branches and accompanying fine vessels which pierce the dorsal part of the prenasal wall. The position of these nerve branches resembles the position of the canals *c. n. va* in *Eusthenopteron*. They are said by Reinbach, however, to be twigs of the r. medialis narium.

The r. palatinus VII (*r. pal*) in *Eusthenopteron* (figs. 60, 61; p. 480) passed first forwards dorsally to the posterior part of the vomer, after which it pierced that bone, leaving it on the anterior part of its ventral face. Within the vomer the nerve bifurcated into two terminal branches, one medial ($r_m pal$) and one antero-lateral ($r_{al} pal$), the latter giving off a lateral branch ($r_l pal$) within the vomer. A corresponding development of the r. palatinus VII is met with in *Rana* (fig. 31; pp. 330—331); also here the r. palatinus pierces the vomer from the dorsal to the ventral side and during this part of its course divides into a medial ($r_m pal$) and an antero-lateral ($r_{al} pal$) terminal branch, the latter giving off a lateral branch ($r_l pal$) ventrally to the vomer. The agreement thus found is so considerable that one is fully justified in concluding that the three terminal branches of the nerve in *Eusthenopteron* must be homologous to the corresponding branches in *Rana*. The fact that in *Eusthenopteron* the lateral terminal branch ($r_l pal$) was given off within the vomer whereas in *Rana* it is sent out ventrally to that bone, is certainly due to the more incomplete development of the vomer in *Rana* (cf. pp. 498—499).

In *Rana* (p. 329) the medial terminal branch ($r_m pal$, fig. 31) of the

r. palatinus VII passes over into the ventral terminal branch of the r. medialis narium (r_vmn), forming the prenasal anastomosis (*ast. pren*). From this anastomosis there issue fine branches ($rr.\ Pmx_3$), inter alia to the mucous membrane lining the pars palatina of the "premaxillary". In *Eusthenopteron* the medial terminal branch of the r. palatinus VII and the ventral terminal branch of the r. medialis narium emerged on the lower face of the cranium fairly close together (through the foramina c_vn-*b* and c_mpal, fig. 56) and it is thus very likely that as in *Rana* they passed over into one another and formed a prenasal anastomosis (*ast. pren*, figs. 60, 61; p. 480). The nerve branches ($rr.\ NRP_3$) in *Eusthenopteron* that pierced the pars palatina of the naso-rostro-premaxillary were probably given off from this anastomosis and thus corresponded to the branches $rr.\ Pmx_3$ in *Rana*. The antero-lateral terminal branch of the r. palatinus VII in *Eusthenopteron* ($r_{al}pal$, figs. 60, 61) emerged in the hindmost part of the prenasal pit postero-medially to the anterior orifice of the anterior palatonasal canal (c_ap-*n*, fig. 56). Since this canal in all probability transmitted a nerve (*r. p-n*) homologous to the r. palatonasalis in the frog, it is highly conceivable that quite as in the frog the antero-lateral terminal branch of the r. palatinus passed over into the r. palatonasalis to form a prechoanal anastomosis (*ast. prech*, figs. 60, 61; p. 480).

The r. ophthalmicus lateralis and r. buccalis lateralis in *Rana* (pp. 331—332) are present in larvae only, in which the skeleton of the snout is still very imperfectly developed, so that the relations of the nerves to the skeletal elements cannot be established. Their topographic relations, therefore, cannot be compared with those of the corresponding nerves in *Eusthenopteron* (pp. 476, 479—480; *r. o lat*, *r. buc*, figs. 59—61). It is worthy of mention, however, that the restoration of the nervous system of the head in the tadpole carried out by Strong (1895, pl. 12, fig. A) shows the r. ophthalmicus lateralis with the same curvatures in the snout as the preorbital part of the supraorbital sensory canal in *Eusthenopteron* (*soc*, fig. 34; cf. *gr. soc*, figs. 47 A, 59). It should also be pointed out that the r. buccalis lateralis in larval stages of the frog is traceable forwards to the tip of the snout, which must mean that there is a row of neuromasts corresponding to the ethmoidal commissure of the infraorbital sensory canals in *Eusthenopteron*. In fishes in general the r. buccalis lateralis is accompanied by a strong maxillaris branch (figs. 2, 9, 10 D, 15; cf. Coghill 1902, pp. 260—261), but this is not the case in *Rana* (Strong 1895, pl. 12) nor was it in *Eusthenopteron* (figs. 60, 61), which in this respect was very much as *Rana*.

The snout in *Eusthenopteron* presents very few canals for vessels only. One of these canals ascends from the olfactory canal a little behind the nasal cavity. This canal (*c. cut. va*, fig. 57; pp. 469—470) gives off branches to the overlying dermal bones in the ethmoidal shield and to the nasal cavity. The vessel which traversed this canal must either have come from or gone backwards to the cranial cavity and it is therefore likely that it was a branch of one of the vessels of the brain. No corresponding vessel seems to be known in *Rana* (cf. ECKER-WIEDERSHEIM-GAUPP 1899, pp. 298, 392; figs. 85, 119; SOCHA 1930). On the other hand, in *Megophrys* and *Scaphiopus* (RAMASWAMI 1935 a, p. 78, figs. 7 a, 8) there is dorsally to either olfactory nerve a fairly strong vessel, probably a vein, which may possibly correspond to the vessel in *Eusthenopteron* now discussed. Another vascular canal in *Eusthenopteron* (*c. ca*, figs. 47 A, B, 57 A, C; p. 469) leads from the anterior dorsal part of the cranial cavity to the orbit and was presumably traversed by the v. cerebralis anterior. In *Rana* such a vein is present only in larvae p. 333). A third vascular canal (*c. a. obl*, fig. 55; pp. 474—476) is formed between the pars autopalatina of the palatoquadrate and the postnasal wall and leads from close behind the posterior orifice of the palatine canal upwards towards the pit (*fo. m. obl*) in which the oblique muscles of the eye probably had their origin. Comparisons with *Rana* show that it may have given passage to an ascending twig of the a. palatina corresponding at least to that twig of the rr. musculares et glandulares in the frog that supplies the m. obliquus inferior (ECKER-WIEDERSHEIM-GAUPP 1899, p. 296, fig. 85).

Since in the snout of *Eusthenopteron* there are only a few canals which were developed exclusively for vessels, the main vessels of the snout in this form must have accompanied the nerves (pp. 480—481). The vascular system of the snout in *Eusthenopteron* must therefore also in all essentials have been as in *Rana* (p. 333) and not as in *Porolepis* and Urodeles (cf. pp. 307—308, 378, 395). We can thus gather that also the vascular system of the snout in the *Osteolepiformes* resembled that system in the *Anura*.

It now remains only to compare the dermal bones of the snout in *Eusthenopteron* and Anurans. The naso-rostro-premaxillaries ("premaxillaries"), the vomers and the parasphenoid have already been treated above (pp. 496—500) in connection with related parts of the endoskeleton. For details concerning the dermal bones in Anurans the reader is referred to works by DUGÈS (1835); W. K. PARKER (1871; 1876; 1881), HOFFMANN (1873—78), ECKER-WIEDERSHEIM-GAUPP (1896—1904), GAUPP (1905), BHATIA and PRASHAD (1918), BOLKAY (1919), DE VILLIERS (1929—1934), C. A. DU TOIT (1930—38), G. P. DU TOIT (1933), ERDMANN (1933), RAMASWAMI (1934—39), STADTMÜLLER (1936), DE BEER (1937), REINBACH (1939), PATERSON (1939, 1939 a), and others.

The maxillary in *Eusthenopteron* (*Mx*, Mx_1, Mx_2, Mx_3, *pr. Mx*, figs. 34, 55, 56, 64 A, 65 A, 68 A, 87 A; pl. 7, fig. 1; pl. 9, fig. 1; pl. 12, figs. 3—6; pl. 13) is certainly a true homologue of the maxillary of Anurans (figs. 22 E, 23, 27, 30, 31, 64 B, 65 B, C, 66, 68 B, C, 69). The bone as a rule extends further forwards in Anurans than in *Eusthenopteron* (cf. p. 497) besides which its pars facialis is more strongly developed in the former than in the latter. We must assume, therefore, that the maxillary developed progressively in the Anurans, both forwards and, in its anterior part, upwards (see figs. 65, 68). In connection with this progressive development of the bone in Anurans a pars palatina (Mx_3) also developed.

The lachrymal in *Eusthenopteron* (*La*, figs. 34, 55, 65 A, 68 A; pl. 7; pl. 9, fig. 1; pl. 12, figs. 3—6; pl. 13) is a large bone overlapping both a large area of the fronto-ethmoidal shield (the larger part of the area *od. La* + *Mx*, fig. 68 A) and a considerable area along the dorsal margin of the maxillary (*od. La*, fig. 68 A). It is a sensory canal bone; its ventral part is pierced throughout its rostro-caudal extent by the infraorbital sensory canal (*ioc*, figs. 34, 55; pl. 9, fig. 1). It consists of a posterior comparatively low division ventrally to the orbital opening (*fe. o*, fig. 68 A) and an anterior higher division in front of the orbital opening. The posterior division takes part in the formation of the anterior part of the lateral wall of the orbit and is attached above the maxillary to the outside of the dermopalatine and along a very narrow zone also to the dorsally curved lateral part of the pars autopalatina of the palatoquadrate (see fig. 55). The anterior division of the bone, attached to the ethmoidal shield, is partly situated outside the postero-ventro-lateral portion of the ethmoidal region, but is separated from that by the overlapped area of the fronto-ethmoidal shield (the area *od.La* + *Mx*, fig. 68 A). The lachrymal in Anurans has hitherto been known only in *Rana pipiens* (W. K. PARKER 1881, pl. 8, figs. 1, 3), but may perhaps be present also in the specimen of *R. esculenta* reproduced in fig. 23 (*La*?)[1]. It is a long low bone situated immediately above the maxillary and covers the outside both of the dorso-lateral part of the palatoquadrate bar and of an adjacent part of the ethmoidal region (cf. figs. 65 B, 68 B). Its position is thus obviously much the same as that of the lachrymal in *Eusthenopteron* and though vestigial it must certainly correspond to that bone[2].

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[1] This specimen of *R. esculenta* is badly damaged behind the snout and it is thus impossible to make sure whether in this case we are actually concerned with a lachrymal.

[2] Since an independent lachrymal is thus present at least in *Rana pipiens* the maxillary in *Rana* cannot, as maintained by SÄVE-SÖDERBERGH (1936, p. 156, fig. 62; cf. 1935, pp. 16, 58, 118—119), be a compound lachrymo-maxillary.

Of the lateral rostral in *Eusthenopteron* (pp. 449—450) and *Osteolepiformes* in general (*R. l*, *R. l. pal*, *pr. dim*, $pr.\ dim_{rc}$, figs. 34, 52 B, 53, 58, 62 B, 63, 68 A, 70 A, 71 A, 72 A, 86 A) normally only the processus dermintermedius persists in Anurans (see pp. 529, 532—535), where it forms the septomaxillary (*Smx*, Smx_{am}, Smx_{pl}, figs. 22 E, 27 A, 29, 68 B, C, 69, 70 B, C, 71 B, C, 72 B, C; pp. 317—319). In certain Anurans, however, there is also a vestige of the pars facialis of the lateral rostral of the *Osteolepiformes*, the external lamina of the septomaxillary (Smx_{fa}, figs. 68 B, 71 B; cf. p. 516). The larger part of the pars facialis and the entire pars palatina of the lateral rostral are absent in Anurans.

The anterior tectal in *Eusthenopteron* (pp. 448—449; *Te. a*, *pr. Te*, figs. 34, 52 B, 53, 58, 68 A) is a fairly large bone forming the dorsal boundary of the fenestra exonarina anterior. It closes the dorsal part of the fenestra endonarina anterior and covers the dorsal part of the lateral nasal wall above and behind that fenestra and also an adjacent part of the tectum nasi. Its centre of radiation lies somewhat behind the middle of the bone, postero-dorsally to the fenestra exonarina anterior and slightly above the dorsal margin of the fenestra endonarina anterior. The so-called "nasal" in Anurans ("*Na*", figs. 22 E, 23 A, 27 B, 30, 66, 68 B, C, 69) varies in aspect, but in certain forms, e. g. *Phryniscus* (W. K. PARKER 1881, pl. 41, figs, 1, 3, 6, 8), it agrees both in shape and position fairly well with the anterior tectal in *Eusthenopteron* and just like that also forms the dorsal boundary of the fenestra exonarina anterior. The primordium of the "nasal" in Anurans arises close dorsally to the posterior part of the fenestra endonarina communis and thus lies at about the same place in relation to the nasal capsule as the centre of radiation of the anterior tectal in *Eusthenopteron*. The "nasal" in Anurans thus agrees on the whole so closely with the anterior tectal in *Eustenopteron* that there is reason to suspect it to be the exact homologue of that bone (cf. pp. 345, 415). Contrary to the anterior tectal in *Eusthenopteron*, however, it is, as far as known, devoid of an medially directed process (*pr. Te*).

The complex supraorbito-tectal in *Eusthenopteron* (*So-Te*, figs. 34, 55, 65 A, 68 A; pl. 6, fig. 2; pls. 7, 10; p. 351) seems to be without equivalents in recent Anurans, but it may possibly be represented by the so-called prefrontal in the oldest known fossil frog, *Protobatrachus*. from the Lower Triassic (PIVETEAU 1937; WATSON 1940, fig. 18; cf. "*Pfr*" figs. 65 B, 68 B in this work).

Of the nasals in *Eusthenopteron* (*Na*, Na_1—Na_7 figs. 34, 50, 52 B, 53, 55, 58, 65 A, 68 A; pl. 6, fig. 1; pl. 7; p. 349) only the foremost one incorporated in the "premaxillary" or naso-rostro-premaxillary seems to be represented in Anurans. The so-called "nasal" in Anurans is, as we have seen, presumably a homologue of the anterior tectal in *Eusthenopteron.*

Equivalents to the postrostrals in *Eusthenopteron* (*Ptr*, Ptr_m, Ptr_a, figs. 34, 50, 53, 55, 58, 65 A, 68 A; pl. 6, fig. 1; pl. 7, fig. 2; pl. 11, figs. 3—5; pl. 12, fig. 5) are probably generally absent in Anurans. However, both in *Calyptocephalus* (REINBACH 1939, pp. 321—323; "derm-internasofrontale") and *Xenopus* (GILCHRIST and v. BONDE 1919; see PATERSON 1939, p. 184; "supraethmoid") there is an unpaired median bone so situated that it may possibly be a vestigial posterior median postrostral (cf. Ptr_m, figs. 65 A, B, 68 A, B).

As shown above (pp. 343—344), the frontal in *Eusthenopteron* (*Fr*, figs. 34, 50, 55, 65 A, 68 A; pl. 7) corresponds to the frontal component of the complex fronto-parietal in Anurans (*Fr-Pa*, figs. 23 A, 24, 69; cf. *Fr*, figs. 65 B, 68 B; *Fr-Pa*, figs. 65 C, 68 C).

The dermopalatine in *Eusthenopteron* (*Dpl*, *la. Dpl*, figs. 54—56, 60, 64 A, 65 A, 87 A; pp. 453—454) covers the lower face of the antero-lateral and lateral parts of the pars autopalatina of the palatoquadrate and forms the postero-medial boundary of the fenestra exochoanalis. Its foremost end rests on the dorsal face of the vomer. In Anurans the dermopalatine (*Dpl*, figs. 23, 66; cf. figs. 64 B, 65 B, C) has the same position in relation to the choana as in *Eusthenopteron* and also overlaps the vomer from above in certain forms (*Pseudohemisus*, *Scaphiophryne*; NOBLE and PARKER 1926, figs. 13 D, 14 D). In adult Anurans the dermopalatine, as we have seen above (p. 524), covers the lower side of the postnasal wall, presumably due to a fusion between the antero-lateral part of the palatoquadrate and the primary postnasal wall. As a whole it is far weaker developed in Anurans than in *Eusthenopteron.* In Anurans it is also generally devoid of a vertical descending tooth-bearing lamina corresponding to the one found in *Eusthenopteron* (*la. Dpl*, fig. 64 A). However, a somewhat similar lamina exists in certain forms, e. g. *Bufo* (*la. Dpl*, fig. 66; cf. figs. 64 B, 65 B), but is merely a ventral ledge without teeth.

As compared with the entopterygoid in *Eusthenopteron* (*Enpt*, figs. 54 A, 55, 56, 64 A, 65 A, 87 A) the entopterygoid in Anurans (figs. 23, 66; cf. figs. 64 B, 65 B) is much reduced anteriorly.

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The comparisons now made show plainly that as regards the anatomy of the snout there are numerous highly important points of agreement between *Osteolepiformes* and *Anura.* Most of them are so striking and of such a fundamental nature that they cannot in any way be explained as parallelisms. The snout in *Osteolepiformes*, though primitive, is beyond doubt of a fundamentally Anuran type. The differences between *Osteolepiformes* and *Anura* in the structure of the snout are practically all due to secondary modifications in the Anurans, above all a regressive development of the skeleton. From the comparisons with other groups of fishes and Urodeles (pp. 488—495) it is obvious that the *Osteolepiformes* differ considerably from all these groups with regard to the snout, and, as will be shown below (pp. 593—597), their snout is also very different from that in Coelacanthids. We are then fully justified in concluding 1) that the *Osteolepiformes* are very closely related to the Anura, and 2) that the *Osteolepiformes* include or at any event are very near to the ancestors of the Anura. These results as to the relationship of the *Osteolepiformes* are in full agreement with those gained by Holmgren (1933, 1939) in his studies of the skeleton of the paired fins (cf. foot-note 1 on p. 493) and in the main also with those arrived at by Säve-Söderbergh (1936, pp. 136—168) in his comparisons between *Rhizodopsis*, *Labyrinthodontia* and the tadpole.

The most important characters in the snout of the *Osteolepiformes* proving that they are very closely akin to the *Anura* may be summarized as follows (cf. the points of agreement between *Porolepiformes* and *Urodela*, pp. 417—421, and the differences between *Porolepiformes* and *Osteclepiformes*, pp. 489—493).

1) The internasal wall is comparatively narrow and forms a solid septum nasi continued backwards by a septum between the canales olfactorii. It houses neither a cavum internasale nor any anterior part of the cranial cavity.

2) The divisio prenasalis communis is provided with a crista subnasalis homologous to that in Anurans. On the lower side of the divisio prenasalis communis and on the antero-lateral part of the vomer there is a paired pit, the prenasal pit, which represents an initial stage towards the development of the prenasal and subnasal cavities in Anurans. The divisio prenasalis communis is pierced by the branching nasobasal canal which gave passage to nerves and vessels homologous to those traversing, the fenestra nasobasalis and the cavum prenasale in Anurans.

3) The prenasal pits probably housed a gland homologous to the intermaxillary gland in Anurans. The efferent ducts of this gland passed backwards and united into a common efferent duct as in *Arthroleptides*.

4) The nasal cavity occupies a similar position in the ethmoidal region as in Anurans and is situated comparatively close to that of the opposite side (cf. No. 1).

5) The nasal capsule is approximately complete as in larvae of certain

Anurans and as in certain adult Anurans. The lamina nariochoanalis is made up of the anterior ventral part of the lateral nasal wall only.

6) The fenestra endonarina anterior is large and agrees well in position and shape with the corresponding part of the fenestra endonarina communis in Anurans.

7) The fenestra endonarina posterior is situated in the ventro-lateral part of the postnasal wall and is bounded by a thin lateral wall, which probably partly consisted of cartilage. At the corresponding place in Anurans a distinct notch is developed for the nasolachrymal duct in the lateral margin of the postnasal wall.

8) The solum nasi is imperfectly developed, its larger posterior and lateral part is entirely occupied by the large fenestra endochoanalis.

9) Only a single nerve canal (for the r. externus narium) ascends from the nasal cavity. This canal corresponds to the foramen frontale in Anurans.

10) The postnasal wall is pierced by a comparatively narrow profundus canal which may bifurcate into two branches, lateral and medial. Lateral profundus canals are absent.

11) There is no equivalent to Seydel's palatal process of the *Porolepiformes* and Urodeles.

12) Through formations homologous to the crista intermedia, lamina superior, lamina inferior and septomaxillary of the Anurans the nasal cavity is subdivided into three compartments corresponding to the recessus superior, recessus medius and recessus inferior of the Anurans. In addition two other recesses are also developed in the nasal cavity, one lateral and one ventro-medial. The lateral recess corresponds to the lateral recess of the Anurans and must have housed a lateral diverticle of the nasal sac corresponding to the diverticulum laterale in Anurans. The ventro-medial recess must have housed a part of the nasal sac homologous to the diverticulum mediale (Jacobson's organ) in Anurans.

13) The lateral recess is bounded, as in Anurans, by the postero-ventral medially curved part of the lateral nasal wall. Just as in the Anurans there is no equivalent to the crista rostro-caudalis, so characteristic of *Porolepiformes* and Urodeles.

14) The posterior external nasal tube had its posterior orifice in the foremost part of the orbital opening close in front of the eye-ball and was thus developed as a nasolachrymal duct. Its position in relation to the postnasal wall was fundamentally as in Anurans. The tube in question was situated dorsally to the processus dermintermedius of the lateral rostral (septomaxillary) just as in larvae of certain Anurans (*Calyptocephalus*).

15) The great agreement in the development of the nasal cavity shows that the nasal sac must have been fundamentally of an Anuran type.

16) The forebrain was very much as in Anurans. The bulbi olfactorii lay close to one another in front of the hemispheres.

17) The lateral parts of the snout were innervated by the r. maxillaris V, which was a strong nerve developed very much as in Anurans.

18) The vascular system of the snout was certainly in all essentials as in Anurans. The lateral parts of the snout received their blood-supply and wery drained by vessels accompanying the branches of the r. maxillaris V.

19) The n. profundus was not very powerfully developed. Its branching and the relations of its branches to the skeleton were almost exactly as in *Rana*.

20) The r. palatinus VII pierced the vomer and as in *Rana* it broke up in that bone into one medial and one antero-lateral branch, the latter giving off a lateral branch. Also the r. ophthalmicus lateralis and the r. buccalis lateralis seem to have been approximately as the corresponding nerves in Anurans. The four nerve anastomoses found in *Rana* probably existed also in *Eusthenopteron*.

21) The palatoquadrate was, as in Anurans, rigidly connected with the endocranium at the corner between the postnasal and interorbital walls. Most probably there was a synchondrotic connection. The foremost lateral part of the palatoquadrate is provided with a process, the processus dorso-lateralis, whose lateral side abuts against the medial side of the processus ventro-lateralis of the postnasal wall. These processes agree in every respect with the processus quadrato-ethmoidalis and the processus maxillaris posterior in larvae of Anurans. On the whole the anterior and antero-lateral parts of the pars autopalatina of the palatoquadrate are very much as the commissura quadrato-cranialis anterior in larvae of Anurans and probably correspond to that.

22) The naso-rostro-premaxillary agrees in position and shape with the "premaxillary" of Anurans and is certainly homologous to that bone. Anteriorly the two partes palatinae form a median process pointing backwards. The lateral part of the pars palatina is provided with a lateral process which rests against the medial side of the crista subnasalis.

23) The parasphenoid is narrow and extends forwards underneath the transition of the internasal wall into the divisio prenasalis communis.

24) The vomers are in position and shape fundamentally as in Anurans. They are thus provided with descending tooth-bearing laminae

which together form the chief posterior boundary of a distinct fossa apicalis in the foremost part of the roof of the mouth cavity. Each vomer also has an antero-lateral process which meets the pars palatina of the naso-rostro-premaxillary, and it is, as in certain Anurans (*Ascaphus*), produced into a posterior process extending backwards along the parasphenoid.

25) The anterior palatal fenestra is a transverse opening in the dermal skeleton of the roof of the fossa apicalis in front of the vomers and underneath the divisio prenasalis communis.

26) There were probably muscles corresponding to the m. medialis narium and m. lateralis narium of the Anurans.

27) There was in all probability also a m. levator bulbi, differentiated inter alia into a portio principalis and a portio transversalis, both inserted, as in larvae of Anurans, into the palatoquadrate.

28) The oblique muscles of the eye probably arose close to each other in the ventral part of the antero-medial corner of the orbit.

D. The snout in Coelacanthiformes.

1. Descriptive section.

a. The genera Euporosteus Jaekel, Nesides Stensiö, and Diplocercides Stensiö.

(Figs. 73—79; pls. 14—16.)

Previous investigations. — The snout in Devonian Coelacanthids, especially its endoskeleton, has hitherto been imperfectly known.

The endocranium of *Diplocercides kayseri* (v. Koenen) was described by Stensiö in 1922 (pp. 169—186, figs. 1—4; pl. 3, figs. 1—4; pl. 4; pl. 5, figs. 1, 2), but Stensiö (1932, p. 25) has later pointed out that his account of the ethmoidal region was erroneous in several respects. It is of interest that the lateral nasal wall in *Diplocercides* was found to be pierced just behind the fenestra endonarina communis by a canal running antero-dorsally (Stensiö 1922, pp. 185—186; *lat. for*, fig. 1), which gave passage to the r. maxillaris V and the r. buccalis lateralis. The endocranium has also been dealt with both in *Euporosteus eifelianus* Jaekel (Jaekel 1927, pp. 915—916, figs. 23, 49; Stensiö 1937 a, figs. 9, 10; pl. 11, figs. 3, 4; pl. 12) and in *Nesides schmidti* Stensiö[1] (Stensiö 1932, figs. 8, 11, 14; 1937 a, figs. 5, 8, 22; HOLMGREN and STENSIÖ 1936, pp. 345—353, figs. 266, 269 B), but no description of the ethmoidal region has been given. The general features of this region in these two forms and the position of the nasal cavities are, however, plainly shown in certain of the figures published of the endocranium. STENSIÖ (1922, p. 189; pl. 5, fig. 1) has shown that the anterior part of the palatoquadrate in *Diplocercides* forms a separate autopalatine ossification. This part of the palatoquadrate is unknown in *Euporosteus* and *Nesides*, but there is every reason to assume that it was fundamentally as in *Diplocercides*.

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[1] The genus *Nesides*, earlier confused with *Diplocercides*, was distinguished in 1937 Stensiö 1937 a).

The sensory canal system and dermal bones of the skull in *Diplocercides*, *Euporosteus* and *Nesides* were described by STENSIÖ (1922; 1937 a), but in the snout they are still unsatisfactorily known.

Material. — The present account of the snout in Devonian Coelacanthids is based on the following material: 1) the holotype of *Euporosteus eifelianus* (Geological-Palaeontological Institute of the University of Berlin); 2) the holotype of *Nesides schmidti* (Geological-Palaeontological Institute of the University of Göttingen; STENSIÖ 1937 a, pl. 9; pl. 10, figs. 2, 3), with a series of drawings of transverse grinding-sections (SOLLAS' grinding method; intervals between sections drawn 0,1 mm) and models in wax of the endocranium; 3) the holotype of *Diplocercides kayseri* (Geological-Palaeontological Institute of the University of Göttingen; STENSIÖ 1937 a, pl. 1; pl. 10, fig. 1); 4) *Diplocercides kayseri*, specimen a (Geological-Palaeontological Institute of the University of Berlin; STENSIÖ 1937 a, p. 38; pl. 2).

The holotype of *Euporosteus eifelianus* consists of the ethmosphenoid with the parasphenoid and remains of certain of its other dermal bones. The holotype of *Nesides schmidti* shows the posterior tectal. The endocranium of this specimen studied by SOLLAS' grinding method was well preserved, apart from the ethmoidal region which was imperfect in its median and antero-dorsal parts and on the left side (see fig. 76). The specimens of *Diplocercides* show inter alia a cast of the nasal cavity and the lateral rostral.

Description. — The following description deals above all with *Euporosteus* and *Nesides*, in which the snout is much more completely preserved than in *Diplocercides*.

As in *Porolepiformes* and *Osteolepiformes* the endocranium in the three genera mentioned is occupied by two large unpaired ossifications, an otico-occipital and an ethmosphenoid. The ethmosphenoid (cf. STENSIÖ 1937 a, figs. 5, 8) shows practically only perichondral bone layers, which line the outer faces of the interorbital wall, large parts of the outer faces of the ethmoidal region and to a large extent also the cavities and canals both in the interorbital wall and the ethmoidal region. The interior of the ethmosphenoid was thus chiefly or at least to a large extent filled with cartilage, and the endocranium is much less strongly ossified than in *Porolepiformes* and *Osteolepiformes*.

The perichondral bone layers of the ethmosphenoid extend forwards to the rostral end of the ethmoidal region, but it is obvious that they were absent in places. This is above all the case in the internasal wall, which consisted practically entirely of cartilage. Both in *Diplocercides* and *Nesides* the perichondral lining of bone on the anterior parts of the ventral side of the ethmoidal region is also partly vestigial or absent (fig. 74 B). In *Nesides* it is also seen that the perichondral bone layer is absent on certain external parts of the postnasal wall (figs. 75 B, 76).

In *Nesides* the ethmoidal region covers about one fourth of the total length of the endocranium and about $^2/_5$ of the ethmosphenoid, but in *Euporosteus* it is somewhat longer, its length there being about half of the total length of the ethmosphenoid. In both the ethmoidal region is broader than long, but longer than high, and broadest in its posterior part just in front of its transition into the interorbital wall. The proportions between its breadth, length and height are in *Nesides* about 5 : 3 : 2 and in *Euporosteus* about 4 : 3 : 2.

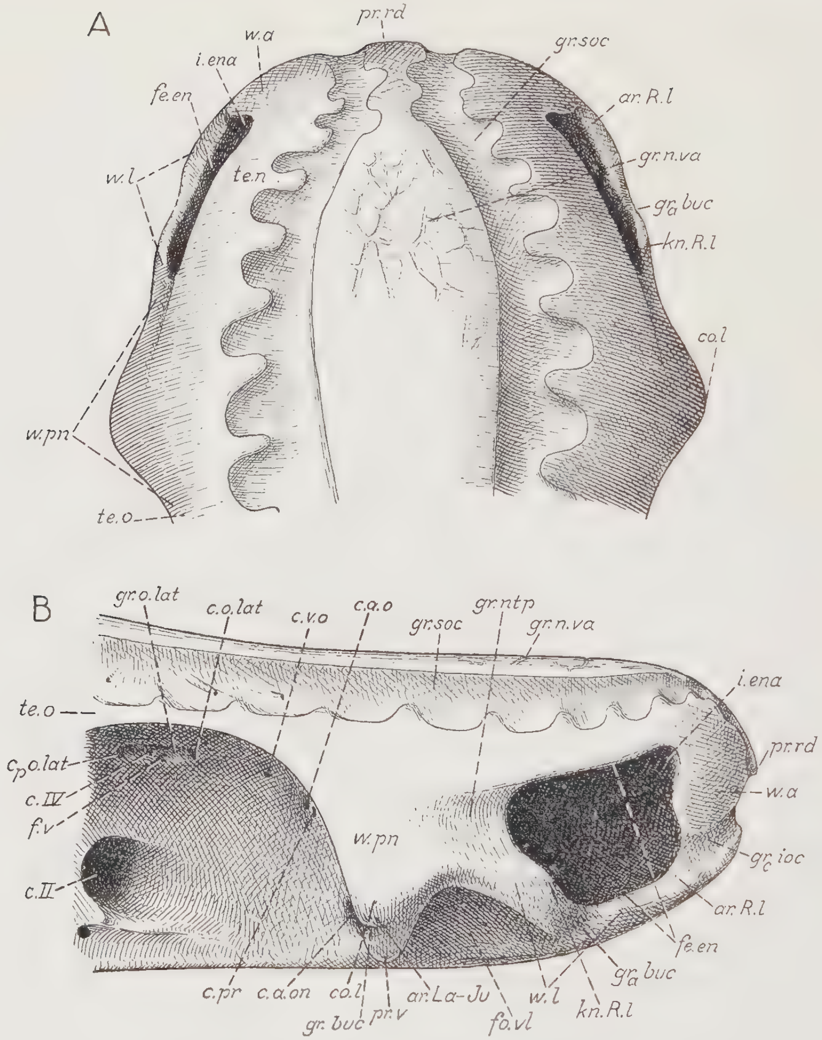
In its essential characters the ethmoidal region is developed very much in the same way in the three forms. It has an upper face, a lower face, and a paired posterior face. These three faces meet postero-latero-ventrally on either side to form an obtuse lateral corner (*co. l*, figs. 73—76), which is the most laterally protruding part of the region. The postnasal wall (*w. pn*, figs. 73—76, 79), on the whole transverse in position, is very thick and strong. Its antero-latero-ventral part has a large fossa, the ventro-lateral fossa (*fo. vl*, figs. 73 B, 74, 76 B, C). The internasal wall (*w. in*, fig. 76 A) is fairly narrow ventrally but was certainly thicker in its upper parts, above all posteriorly. Most probably a median rostral cavity (*cav. rm*, fig. 79) was contained in it. The nasal cavity is not particularly large (*cav. nc*, figs. 76 A, 78 A, 79); it lies comparatively close to that of the opposite side but strikingly far forwards considering the length of the ethmoidal region. It opens outwards through a large opening in the lateral nasal wall, the fenestra endonarina communis (*fe. en*, fig. 73). No fenestra endochoanalis is developed. The divisio prenasalis communis (*w. pren*, fig. 79) is solid and is not pierced by any wide canals.

The foremost part of the orbitotemporal region forms a thick interorbital wall (figs. 73 B, 75, 76 B), which dorsally on either side bears a well developed tectum orbitale (*te. o*, figs. 73, 75).

The anterior part of the palatoquadrate is not preserved in *Euporosteus* and *Nesides* but its autopalatine ossification has been observed, though damaged, in *Diplocercides.* As the anterior part of the palatoquadrate is thus very unsatisfactorily known in all three forms, I shall not enter upon it here (cf. p. 592).

The dorsal face of the ethmoidal region is completely preserved only in *Euporosteus* (fig. 73; pl. 14; pl. 15, fig. 2), where it is developed as follows. The median part of the face is almost plane except most anteriorly, where opposite the anterior end of the fenestra endonarina communis (*fe. en*) it curves strongly downwards so that its foremost part is directed almost straight forwards. The lateral parts have a strong downward curve and thus a decided lateral direction. The groove for the supraorbital sensory canal (*gr. soc*, figs. 73, 74 A, 75, A; pl. 14) is very wide and gives off several lateral, short and broad grooves, which housed excessively developed sensory canal tubes. The foremost parts of the grooves for the supraorbital sensory canals lie pretty close to each other, especially between the anterior ends of the fenestrae endonarinae communes. The foremost ends of the grooves form notches in the anterior end of the ethmoidal region, and thus bound off a median short and narrow rostral process, the dorsal rostral process (*pr. rd*, figs. 73, 74 A; pls. 14, 15). The foremost portion of the median horizontal area of the dorsal face is provided with a network of fine grooves for twigs of nerves and vessels (*gr. n. va*, fig. 73; pl. 14, fig. 1). In the anterior lateral part of the dorsal face we find the large fenestra endonarina communis (*fe. en*, fig. 73), from the postero-dorsal part of which a distinct groove, *gr. ntp* (see p. 564—565), leads backwards. — The dorsal face of the ethmoidal region in the holotype of *Nesides* (fig. 76; cf. fig. 78) was imperfectly preserved but in most respects it seems to have been approximately as in *Euporosteus.* It is probable, however, that as a whole it sloped more forwards than the corresponding face in *Euporosteus* (cf. Stensiö 1932, fig. 8; 1937 a, fig. 3). Unlike that in *Euporosteus* the groove for the supraorbital sensory canal in *Nesides* (*gr. soc*, fig. 76) is devoid of short lateral grooves for tubuli. At the bottom of the groove in *Nesides* there open several fine ascending canals ($c_{d}o.\,lat$, fig. 76 A, C) which once transmitted twigs of the r. ophthalmicus lateralis, n. profundus and vessels. Other canals of this sort (*c. lat*) ascend to the groove further backwards through the tectum orbitale.

The ventral face of the ethmoidal region (fig. 74) differs somewhat as to proportions and other minor features, but is otherwise developed in a similar way in the three Devonian genera here in question. The anterior part of the face curves upwards (fig. 73 B). The posterior lateral parts of the face are directed strongly laterally, due to the presence here of the large and deep fossa ventro-lateralis (*fo. vl*). Antero-laterally to the anterior end of the parasphenoid is a paired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fo.vl

Fig. 73. *Euporosteus eifelianus* Jaekel. Restorations of the anterior part of the ethmosphenoid. *A*, dorsal, *B*, lateral view. $^6/_1$.

ar. La-Ju, area for attachment of anterior end of lachrymo-jugal; *ar. R. l*, area for attachment of lateral rostral; *c. a. on*, canal, probably for an orbitonasal artery; *c. a. o.* canal, probably for a. ophthalmica; *co. l*, lateral corner of ethmoidal region; *c. o. lat*, $c_p o.\ lat$, anterior and posterior canals for r. ophthalmicus lateralis; *c. pr*, anterior profundus canal; *c. v. o*, canal, probably for v. ophthalmica; *c. II*, *c. IV*, canals for n. opticus and n. trochlearis; *fe. en*, fenestra endonarina communis; *fo. vl*, fossa ventro-lateralis of postnasal wall; *f. v*, vein foramen; $gr_a buc$, *gr. buc*, anterior and posterior grooves for r. buccalis lateralis; $gr_c ioc$, groove for ethmoidal commissure of infraorbital sensory canals; *gr. ntp*, groove for the thickened anterior part of the posterior tectal pierced by canal for posterior nasal tube; *gr. n. va*, grooves for twigs of nerves and vessels; *gr. o. lat*, groove for r. ophthalmicus lateralis; *gr. soc*, groove for supraorbital sensory canal ridge; *i. ena*, notch for anterior nasal tube; *kn. R. l*, protuberance for attachment of lateral rostral; *pr. rd*, dorsal rostral process; *pr. v*, ventral process of postnasal wall; *te. n*, tectum nasi; *te. o*, tectum orbitale; *w. a*, *w. l*, anterior and lateral nasal walls; *w. pn*, postnasal wall.

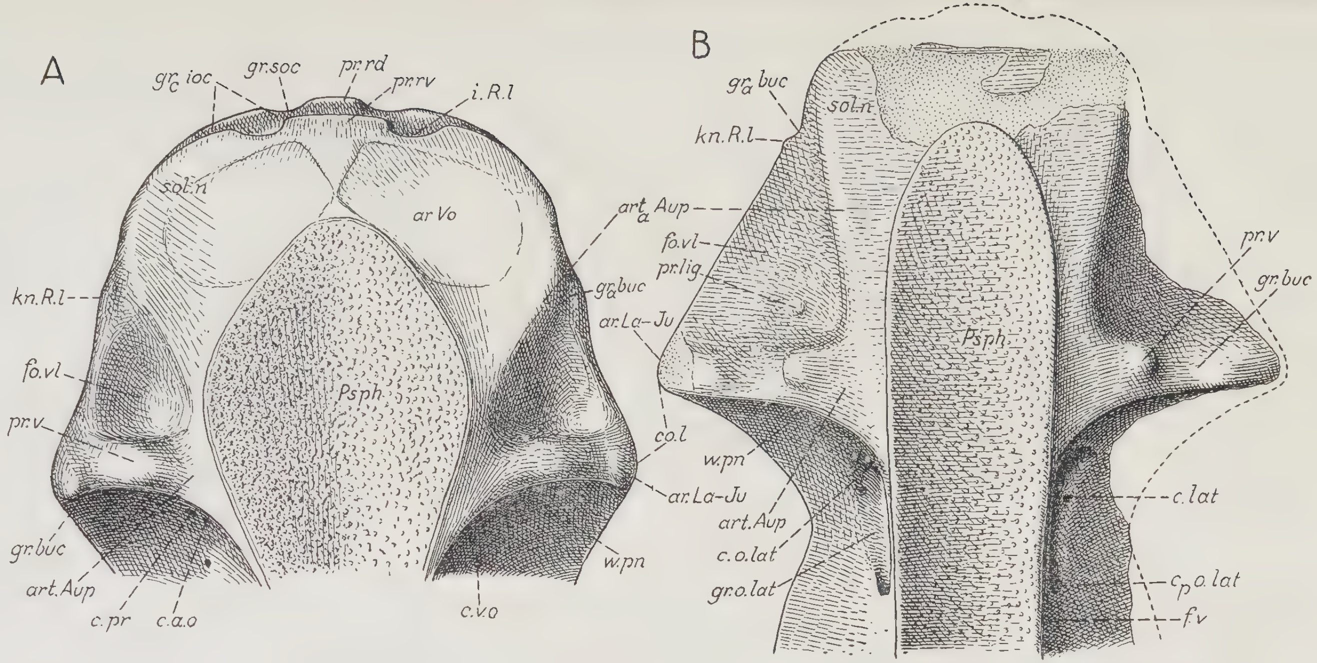
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Fig. 74. Anterior part of the ethmosphenoid with the parasphenoid in ventral view. Cartilage dotted. *A*, *Euporosteus eifelianus* Jaekel. $^6/_1$. *B*, *Nesides schmidti* Stensiö. Graphical restoration after the grinding-series. $^{14}/_3$.

Psph, parasphenoid; *ar. La-Ju*, area for attachment of anterior end of lachrymo-jugal; *art*$_a$*Aup*, facet against which the medial margin of the autopalatine ossification probably abutted; *art. Aup*, autopalatine articular area; *ar. Vo*, vomeral area; *c. a. o*, canal, probably for a. ophthalmica; *c. lat*, canal for branch of r. ophthalmicus lateralis; *co. l*, lateral corner of ethmoidal region; *c. o. lat*, *c*$_p$*o. lat*, anterior and posterior canals for r. ophthalmicus lateralis; *c. pr*, anterior profundus canal; *c. v. o*, canal, probably for v. ophthalmica; *fo. vl*, ventro-lateral fossa of postnasal wall; *f. v*, vein foramen; *gr*$_a$*buc*, *gr. buc*, anterior and posterior grooves for r. buccalis lateralis; *gr*$_c$*ioc*, groove for ethmoidal commissure of infraorbital sensory canals; *gr. o. lat*, groove for r. ophthalmicus lateralis; *gr. soc*, groove for supraorbital sensory canal ridge; *i. R. l*, notch for antero-ventral end of lateral rostral; *kn. R. l*, protuberance for attachment of lateral rostral; *pr. lig*, process, probably for a ligament inserted into the autopalatine ossification; *pr. rd*, *pr. rv*, dorsal and ventral rostral processes; *pr. v*, ventral process of postnasal wall; *sol. n*, solum nasi; *w. pn*, postnasal wall.

depressed area, the vomeral area (*ar. Vo*, fig. 74 A), somewhat elliptical or rectangular in outline. In geologically younger Coelacanthids the vomer is situated on a corresponding area (cf. fig. 81 and p. 583) and it is therefore very likely that it is the area of attachment of that bone. The foremost part of the face is crossed by a transverse groove, *gr_cioc* (figs, 73 B, 74 A; pl. 15), which on either side extends backwards to the antero-ventral corner of the fenestra endonarina communis. This groove, to which leads the groove for the supraorbital sensory canal (*gr. soc*), must have housed the foremost part of the lateral rostral (*R. l*, fig. 77 B, C; pp. 567, 570) and the presumably tube-shaped medial rostrals (cf. fig. 80), and was thus undoubtedly created by the foremost parts of the infraorbital sensory canals and their ethmoidal commissure (*ioc*, pl. 15, fig. 2). The ventral boundary of the groove consists of a marked ledge (figs. 73 B, 74 A). In the medial part of this ledge there is a paired notch (*i. R. l*, figs. 74 A, 77 C; pl. 15, fig. 1) occupied by the foremost part of the lateral rostral. By this paired notch the median part of the ledge is bounded off from the lateral part of either side so as to form a short median process, the ventral rostral process (*pr. rv*, figs. 74 A, 77 C; pl. 15, fig. 1). This process is broader than the dorsal rostral process (*pr. rd*) but does not extend so far forwards as that. The dorsal rostral process thus lies above and the ventral rostral process below the ethmoidal commissure of the infraorbital sensory canals, which passes just ventrally to the very rostral end of the ethmoidal region. No canals for nerves and vessels are found on the ventral face of the ethmoidal region, and, as pointed out before, there is no fenestra endochoanalis.

The ventro-lateral fossa (*fo. vl*, figs. 73 B, 74, 76 B, C; pl. 14, fig. 2; pl. 15) was presumably occupied by an ascending lamina (*la. Aup*) of the autopalatine ossification (*Aup*, fig. 77 B; p. 592). The fossa is developed mainly in the anterior ventro-lateral part of the postnasal wall but in *Nesides* it extends forwards slightly onto the lateral nasal wall. Considered as a whole it opens ventro-laterally and somewhat forwards. It is bounded medially by the very thick postnasal wall, but in *Nesides* most anteriorly also to some extent by the lateral nasal wall. Its dorsal boundary is formed by an antero-laterally projecting thick part of the postnasal wall and its posterior boundary by a high transverse ridge descending from the posterior part of the postnasal wall. In *Nesides* it is devoid of a definite anterior boundary, whereas in *Euporosteus* it is separated there from the nasal cavity by a thin wall passing from above obliquely forwards and downwards. On the transverse ridge of the postnasal wall behind the ventro-lateral fossa is a small process projecting ventrally, the ventral process of the postnasal wall (*pr.v*, figs. 73 B, 74, 75, 76 B, C; pl. 14, fig. 2; pl. 15, fig. 1; pl. 16, fig. 1). Medially to this process lies a slightly depressed area (*art.Aup*, figs. 74, 75; pl. 15, fig. 1) against which the autopalatine ossification of the palatoquadrate (cf. p. 592 and fig. 77 C) must have articulated. This area reaches the parasphenoid medially and is continued forwards along the ventro-medial margin of the ventro-lateral fossa by an indistinct facet (art_aAup, fig. 74; pl. 15, fig. 1) against which the medial margin of the autopalatine ossification probably abutted (cf. p. 592). In *Euporosteus* this facet is somewhat widened anteriorly. Laterally to the ventral process there is a notch-like groove, *gr.buc* (figs. 73 B, 74, 75 A, 76 C; pl. 14, fig. 2; pl. 15, fig. 1; pl. 16, fig. 1), which leads from the orbit to the dorso-lateral part of the fossa ventrolateralis. Immediately dorso-laterally to this groove and thus ventrally to the lateral corner (*co.l*) of the ethmoidal region lies a well-defined facet (*ar.La-Ju*) for the attachment of the preorbital part of the lachrymojugal (*La-Ju*, fig. 77 A, B). From the foremost part of the fossa ventrolateralis a shallow groove, gr_abuc (figs. 73, 74, 76; pl. 14, fig. 2; pl. 15), runs forwards and upwards to the postero-ventral corner of the fenestra endonarina communis. In *Diplocercides* this groove seems to be represented by a short canal which pierces the postero-ventral part of the lateral nasal wall (cf. p. 554, and STENSIÖ 1922, pp. 185—186; *lat.for*, fig. 1). In the postero-dorso-medial part of the ventro-lateral fossa there is a fairly rough area which in *Nesides* may be provided with a small process (*pr.lig*, fig. 76 B, C). On this process and on the rough area a ligament probably arose which extended downwards to be inserted into the ascending lamina of the autopalatine ossification of the palatoquadrate. This ligament must have lain dorso-medially to the r. buccalis lateralis, which, as we shall see, had its passage forwards in the grooves *gr.buc* and gr_abuc.

The paired posterior face of the ethmoidal region (figs. 73 B, 74, 75, 76 B; pl. 14, fig. 2; pl. 15, fig. 1; pl. 16, fig. 1) is developed in essentially the same way at least in *Euporosteus* and *Nesides*. It decreases in height laterally towards the lateral corner (*co.l*) and is on the whole devoid of pronounced elevations or pits. No ridge or thickening is found corresponding to the olfactory ridge (*ri.olf*, figs. 37, 47 B, 48—50) of *Porolepiformes* and *Osteolepiformes*, nor does the face show any traces of an articular area for the palatoquadrate. On the ventro-medial part of the face is a large pit (*c.a.on*, *my.v*, figs. 73 B, 75, 76 B, 78 A) with the posterior orifice of the canal for the orbitonasal artery (*c.a.on*, p. 576) and probably also the place of origin (*my.v*) of the m. obliquus inferior (*m.obl.i*, fig. 78 B). The pit is thus presumably an anterior ventral myodome developed in the hindmost part of the canal for

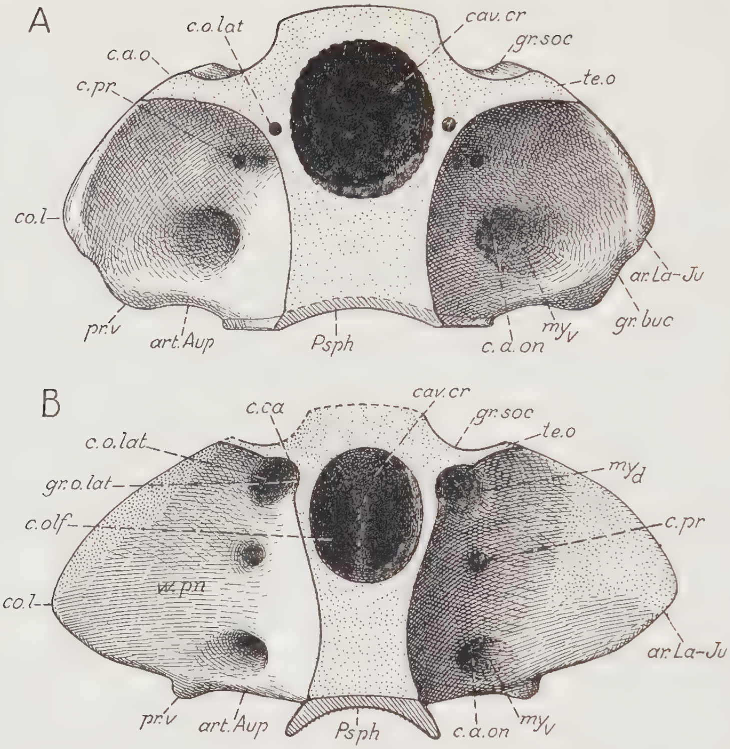

Fig. 75. Restorations of the anterior part of the ethmosphenoid with the parasphenoid. Posterior view. Cartilage dotted. *A, Euporosteus eifelianus* Jaekel. $^{6}/_{1}$. *B, Nesides schmidti* Stensiö. $^{14}/_{3}$.

Psph, parasphenoid; *ar. La-Ju*, area for attachment of preorbital part of lachrymo-jugal; *art. Aup*, autopalatine articular area; *c. a. o*, canal, probably for a. ophthalmica; *c. a. on*, canal, probably for orbitonasal artery; *cav.cr*, cranial cavity; *c. ca*, canal for v. cerebralis anterior; *co. l*, lateral corner of ethmoidal region; *c. o. lat*, anterior canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. pr*, anterior profundus canal; *gr. buc*, posterior groove for r. buccalis lateralis; *gr. o. lat*, groove for r. ophthalmicus lateralis; *gr. soc*, groove for supraorbital sensory canal ridge; my_d, my_v, dorsal and ventral anterior myodomes; *pr. v*, ventral process of postnasal wall; *te. o*, tectum orbitale; *w. pn*, postnasal wall.

the orbitonasal artery. Somewhat above this pit lies the posterior orifice of the anterior profundus canal (*c. pr*). A little further dorsally in *Nesides* we find the posterior orifice of the anterior canal for the r. ophthalmicus lateralis (*c. o. lat*, figs. 74 B, 75 B, 76 B; p. 575).[1] This orifice is widened in a ventro-lateral direction, so that it is much wider than the canal itself (fig. 78 A). In view of this and the course of the n. trochlearis

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[1] In *Diplocercides, Nesides* and *Euporosteus* there is also both a posterior profundus canal and a posterior canal for the r. ophthalmicus lateralis ($c_p o.$ *lat*, figs. 73 B, 76 B), both of which pierce the hinder dorsal part of the ethmosphenoid (Stensiö 1922, pp. 182—184; fig. 1; 1932, fig. 8; 1937 a, pl. 11, figs. 3, 4; pl. 12, fig. 2; Holmgren and Stensiö 1936, p. 350; fig. 266).

(cf. below) it must be assumed that the m. obliquus superior (*m. obl. s*, fig. 78 B) arose in the ventro-lateral part of the orifice in question, which thus is an anterior dorsal myodome (*my. d*). In *Euporosteus* the posterior orifice of the canal for the r. ophthalmicus lateralis is situated pretty far behind the ethmoidal region in the upper part of the lateral face of the interorbital wall (*c. o. lat*, fig. 73 B; pl. 14, fig. 2). In addition to the orifices of canals now dealt with there is in *Euporosteus*, close medially to the posterior orifice of the anterior profundus canal, also a fourth one (*c. a. o*, figs. 73 B, 74 A, 75 A), presumably for the a. ophthalmica (p. 578). This orifice and the orbital orifice of the anterior profundus canal in *Euporosteus* are situated in a common shallow pit, which probably was the place of origin of the m. obliquus superior.

The foremost part of the interorbital wall is comparatively broad throughout its height (cf. STENSIÖ 1937 a, figs. 5, 8) and broadens considerably forwards towards its transition into the ethmoidal region. Its lateral face lacks the olfactory ridge so characteristic of *Porolepiformes* and *Osteolepiformes*. In the upper part of the lateral face is a groove, *gr. o. lat* (figs. 73 B, 74 B, 75 B, 76 B; pl. 14, fig. 2), which connects the posterior and anterior canals for the r. ophthalmicus lateralis (*c_po. lat*, *c. o. lat*). In *Euporosteus* (fig. 73 B) this groove is situated farther forwards than in *Nesides* (fig. 76 B) and shows the openings of two canals which pass outwards from the cranial cavity. One of these canals, maybe the posterior one (*c. IV*, fig. 73 B), transmitted the n. trochlearis, whereas the other one (*f. v*) may have given passage to a vein from the cranial cavity (see p. 579). In *Nesides* the trochlearis canal has its anterior orifice within the anterior part of the posterior canal (*c_po. lat*) for the r. ophthalmicus lateralis. The n. trochlearis must then have continued forwards to the orbit through the latter canal. A canal which presumably transmitted a vein is also developed in *Nesides* (*f. v*, fig. 76 B). It leaves the cranial cavity together with the trochlearis canal but then takes a separate course to the posterior ophthalmicus lateralis canal and continues through the lateral wall of that canal to the orbit. In *Nesides* we also find a canal for a v. cerebralis anterior (*c. ca*, figs. 75 B, 76 B, 78 A) which opens in the very antero-dorsal corner of the orbit. Such a canal was certainly present also in *Euporosteus*, but as it must have opened in the hinder part of the anterior ophthalmicus lateralis canal its external orifice is concealed by the lateral wall of that canal.

The nasal cavity lies strikingly far forwards in the ethmoidal region and at least in its ventral part fairly close to that of the opposite side (figs. 76 A, 79). It is, as we shall see, difficult to make out how the internasal wall is developed. The other nasal walls are completely developed, except the lateral one, which is almost entirely occupied by the large fenestra endonarina communis.

The internasal wall (*w. in*, fig. 76 A; cf. fig. 79) in *Nesides* consisted to a large extent of cartilage. As is shown by the medial extent and configuration of the perichondral bone-layer lining the dorsal face of the solum nasi, this wall was considerably narrower in its anterior than in its hinder ventral parts. Its dorsal parts are not preserved, but certain facts, e. g. the low position of the foremost parts of the olfactory canals (*c. olf*, fig. 76 C) similar to that in *Latimeria* (cf. fig. 83 B), render it very likely that its upper parts may have attained a fairly considerable breadth and lodged an unpaired median rostral cavity (*cav. rm*, fig. 79) as in *Latimeria* (p. 587).

The postnasal wall (*w. pn*, figs. 73—76, 79; pl. 14, fig. 1; cf. pl. 14, fig. 2; pl. 15; pl. 16, fig. 1) is very thick and strongly developed, representing no less than about $^2/_5$ of the total rostro-caudal extent of the ethmoidal region. The anterior face of this wall (fig. 76 C), which constitutes the posterior face of the nasal cavity, is lined with perichondral bone on its ventro-lateral part only and nothing can therefore be said of its special characters. It is clearly seen, however, that the olfactory canal (*c. olf*, fig. 76 C) has its anterior orifice at the ventro-medial corner of this face. Somewhat dorso-laterally to that orifice lies the anterior orifice of the anterior profundus canal (*c. pr*, fig. 76 A, C).

The lateral nasal wall (*w. l*, figs. 73, 76; cf. pls. 14, 15) consists of a high posterior division behind and a low anterior division below the fenestra endonarina communis. The posterior division, which is continuous dorsally with the tectum nasi, posteriorly with the postnasal wall and ventrally with the solum nasi, is almost vertical in position. In *Nesides* it is practically straight, its external face being directed slightly downwards and backwards; in *Euporosteus* it is bent outwards so that its external face is slightly convex in a dorso-ventral direction. The posterior division of the lateral nasal wall forms the posterior boundary of the fenestra endonarina communis and its larger upper part thus has a free anterior margin, which is straight and almost vertical in *Nesides* (fig. 76 B, C), but in *Euporosteus* (fig. 73 B) passes from above obliquely forwards and downwards. In *Euporosteus* it is divided into two parts, upper and lower, by a prominent corner. On the outside of this corner lies a small protuberance (*kn. R. l*, figs. 73, 74 A; pl. 14, fig. 2; pl. 15) for the attachment of the lateral rostral (*R. l*). In *Nesides* this protuberance (*kn. R. l*, figs. 74 B, 76 B, C) lies on the lateral face of the corresponding part of the lateral nasal wall. From the dorsal part of the fenestra endonarina communis in *Euporosteus* above the protuberance just referred to, the wide groove *gr. ntp* (fig. 73 B; pl. 14; pl. 15, fig. 2) runs backwards on the outside of the posterior division of the lateral nasal wall. This groove, which is very imperfectly preserved in *Nesides*, was beyond doubt occupied by a thickened part of the posterior tectal that houses a canal for the posterior external nasal tube (*c.ntp*, pl. 16, fig. 4; see p. 571). The low anterior division of the lateral nasal wall, which forms the ventral boundary of the fenestra endonarina communis, is continuous ventrally with the solum nasi, which it meets almost at right angles. Anteriorly this division passes over into the ledge that forms the ventral boundary of the groove ($gr_{c}ioc$, fig. 73 B) for the rostral bones housing the foremost parts of the infraorbital sensory canals. On the outside of its hindmost part lies the oblique groove $gr_{a}buc$ (figs. 73, 76; p. 561) described above. In front of this groove the dorsal margin of the anterior division is somewhat thickened and bears a facet directed dorso-laterally, *ar.R.l* (figs. 73, 76; pl. 15, fig. 2), against which rests the lateral rostral (cf. fig. 77).

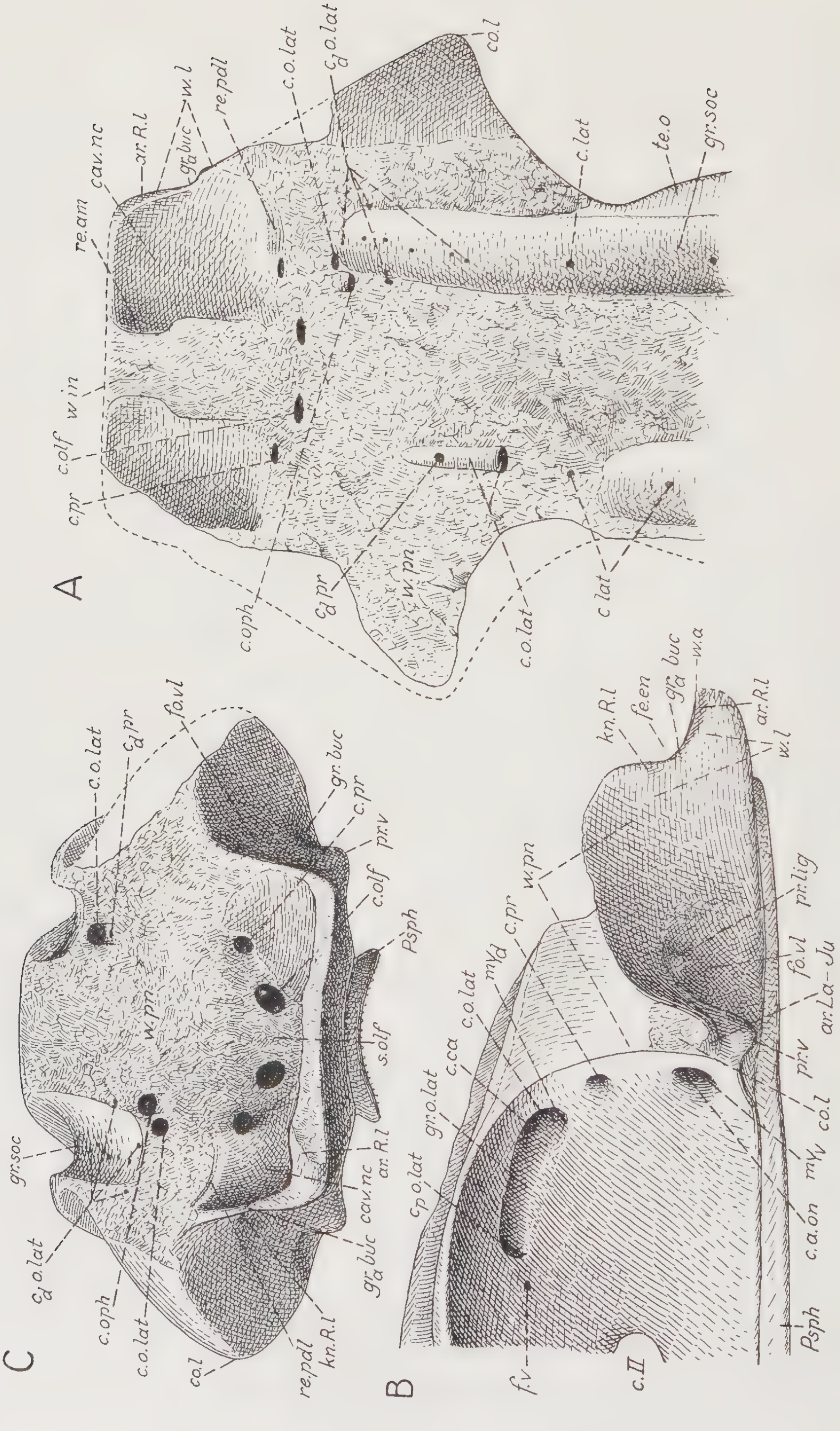
The prenasal wall (*w.a*, figs. 73, 76 A; cf. pls. 14, 15) is formed in the normal way by the lateral part of the divisio prenasalis communis (*w.pren*, fig. 79). Whether it is pierced by any canals could not be made out. Its posterior face, i. e. the anterior face of the nasal cavity, is imperfectly known, but as far as can be seen it is devoid of ridges, crests and processes projecting backwards into the nasal cavity.

The tectum nasi (*te.n*, fig. 73 A; cf. fig. 73 B; pl. 14; pl. 15, fig. 2), preserved only in *Euporosteus*, is thin in its lateral part, which forms the dorsal boundary of the fenestra endonarina communis, but increases in thickness medially towards the internasal wall. It could not be ascertained whether it is pierced by any canals.

The solum nasi (*sol.n*, fig. 74 cf. fig. 76 A; pls. 14, 15) is thin and devoid of canals.

The fenestra endonaria communis (*fe.en*, figs. 73, 76 B, 78 A; pl. 14; pl. 15, fig. 2) is a large opening occupying the larger part of the lateral nasal wall. It is completely preserved only in *Euporosteus* where it is quadrangular in outline, with almost horizontal dorsal and ventral margins. Its anterior margin is as a whole almost vertical whereas the posterior margin slopes from above and behind downwards and forwards. In the upper part of the posterior margin, above the protuberance *kn.R.l*, there is a broad shallow notch for the posterior external nasal tube (*i.enp*, fig. 77 B). Another but narrower and more distinct notch (*i.ena*, figs. 73, 77 B; pl. 14, fig. 1; pl. 15, fig. 2), undoubtedly for the anterior external nasal tube (*nta*, fig. 79; p. 573), is found in the antero-dorsal corner of the fenestra.

Two of the dermal bones of the snout, the lateral rostral and the anterior tectal, are of special interest to us in this connection.


A
re.am
cav.nc
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re.pdl
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te.o
gr.soc
w.in
c.olf
c.pr
c.oph
c$_a$pr
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C
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my$_d$
c.o.lat
c.ca
gr.o.lat
c$_p$o.lat
f.v
c.II
pr.lig
fo.vl
ar.La-Ju
pr.v
co.l
my$_v$
c.a.on
Psph

The lateral rostral[1] is very imperfectly preserved in *Euporosteus* (*R. l*, pl. 15, fig. 2), where it is represented only by an anterior tube-shaped piece lying in the part of the groove $gr_{c}ioc$ (figs. 73 B, 74 A) situated between the fenestra endonarina communis and the ventral rostral process (*pr. rv*). It is also incomplete in *Nesides* (*R. l*, fig. 77 A), where it is shown in the grinding-series in its natural position in relation to the endoskeleton. It is here developed as a tube around the infraorbital sensory canal (*ioc*) and is bent so that in lateral aspect it is convex dorsally and almost correspondingly concave ventrally. Its posterior part is about horizontal, and rigidly and intimately attached to the postnasal wall at the dorsal margin of the fossa ventro-lateralis. The anterior part of the bone, which is incompletely preserved, bends slightly downwards, and is so situated that it closes the ventral part of the fenestra endonarina communis from the outside. It is rigidly attached to the lateral nasal wall at two places: at the protuberance *kn. R. l* (fig. 76 B; cf. fig. 73 B) and at the facet *ar. R. l*. Between these two points of attachment it roofs the groove $gr_{a}buc$ to form a short canal, *c. buc* (fig. 77 A; cf. fig. 77 B, C), leading from behind and below up to the nasal cavity at the posterior ventral corner of the fenestra endonarina communis. Just at this place the lateral rostral is pierced by a fine canal (cf. $c_{1}buc$, fig. 77 C) which ascends to the infraorbital sensory canal and undoubtedly transmitted a branch of the r. buccalis lateralis to a sensory canal organ. A similar canal (cf. $c_{2}buc$, fig. 77 C) ascends through

Fig. 76. *Nesides schmidti* Stensiö. Holotype. Incompletely preserved anterior part of the ethmosphenoid. Restorations from the grinding-series. The larger anterior and dorsal parts of the ethmoidal region are missing. Perichondral bone-layers denoted with ordinary shading, fracture areas with a facet-like shading. *A*, in dorsal view. *B*, in lateral view with parasphenoid. *C*, in anterior view with parasphenoid. $^{5}/_{1}$.

Psph, parasphenoid; *ar. La-Ju*, area for attachment of anterior part of lachrymo-jugal; *ar. R. l*, area for attachment of lateral rostral; *c. a. on*, canal, probably for orbitonasal artery; *c. ca*, canal for v. cerebralis anterior; *cav. nc*, nasal cavity; $c_{d}o.\ lat$, ascending branches of the canal *c. o. lat*; $c_{d}pr$, canal for dorsal branch of n. profundus; *c. lat*, canal for branch of r. ophthalmicus lateralis; *co. l*, lateral corner of ethmoidal region; *c. o. lat*, anterior canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. oph*, canal for branch of v. ophthalmica; $c_{p}o.\ lat$, posterior canal for r. ophthalmicus lateralis; *c. pr*, anterior profundus canal; *c. II*, opticus canal; *fe. en*, fenestra endonarina communis; *fo. vl*, ventro-lateral fossa of postnasal wall; *f. v*, vein foramen; $gr_{a}buc$, *gr. buc*, anterior and posterior grooves for r. buccalis lateralis; *gr. o. lat*, groove for r. ophthalmicus lateralis; *gr. soc*, groove for supraorbital sensory canal ridge; *kn. R. l*, protuberance for attachment of lateral rostral; my_{d}, my_{v}, dorsal and ventral anterior myodomes; *pr. lig*, process for attachment of ligament between postnasal wall and autopalatine; *pr. v*, ventral process of postnasal wall; *re. am*, antero-medial recess of nasal cavity; *re. pdl*, postero-dorso-lateral recess of nasal cavity; *s. olf*, septum between canales olfactorii; *te. o*, tectum orbitale; *w. a*, *w. l*, anterior and lateral nasal walls; *w. in*, internasal wall; *w. pn*, postnasal wall.

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[1] This bone is possibly a complex rostro-tectal (see p. 606).

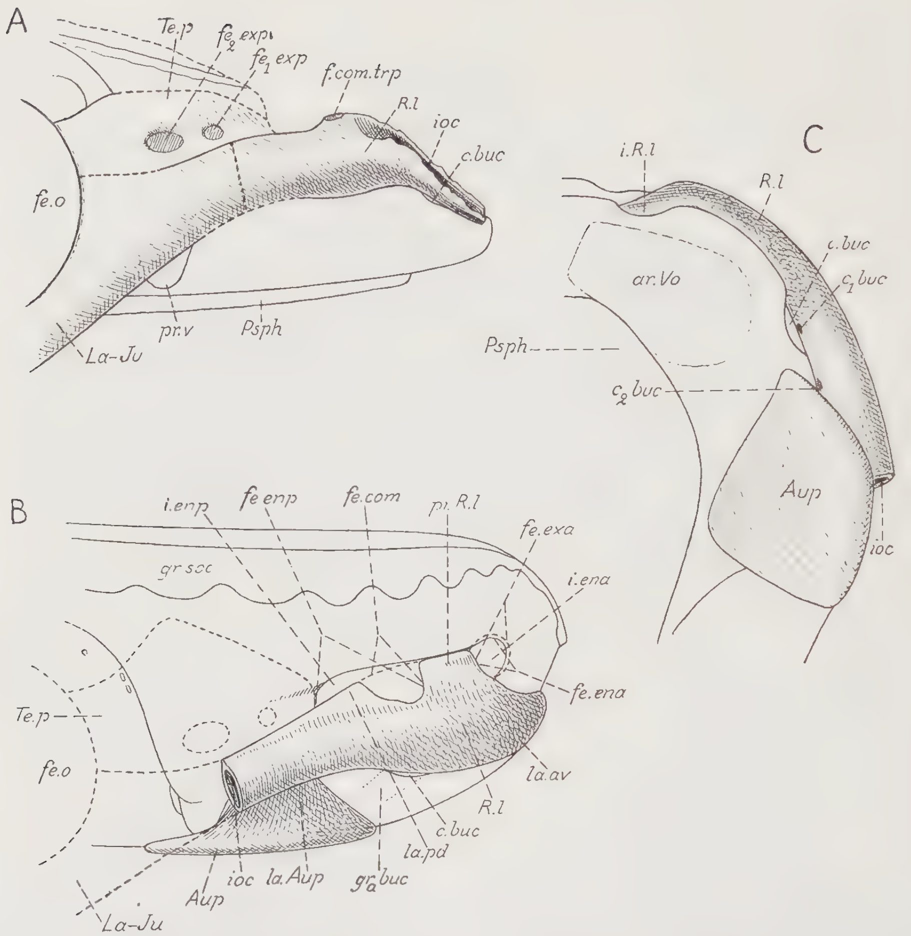

Fig. 77. Restorations showing the position of the autopalatine, lateral rostral (rostro-tectal?) and certain other dermal bones in relation to the anterior part of the ethmosphenoid in Devonian Coelacanthids. *A*, *Nesides schmidti* Stensiö. The anterior part of the endocranium (cf. fig. 76) with certain of the dermal bones in their natural position. Lateral rostral imperfectly preserved. Lateral view. $^{14}/_{3}$. *B*, *C*, the anterior part of the ethmosphenoid of *Euporosteus eifelianus* Jaekel with the lateral rostral of *Diplocercides kayseri* (v. Koenen), the autopalatine of *Latimeria chalumnae* Smith, and, broken lines, the posterior tectal and anterior part of the lachrymo-jugal of *Nesides schmidti* Stensiö. The autopalatine and the dermal bones have been slightly modified so as to fit the endocranium of *Euporosteus*. The prearticular autopalatine part of the palatoquadrate ("pre vomer" of SMITH's description of *Latimeria*) omitted. *B*, lateral view. *C*, ventral view.

Aup, autopalatine ossification; *La-Ju*, lachrymo-jugal; *Psph*, parasphenoid; *R. l*, lateral rostral (rostro-tectal?); *Te. p*, posterior tectal; *ar. Vo*, vomeral area; *c. buc*, canal for r. buccalis lateralis, r. maxillaris V and vessels; c_1*buc*, c_2*buc*, canals for branches of r. buccalis lateralis, *f. com. trp*, foramen, probably for large ascending tube of infraorbital sensory canal (this tube presumably corresponds to the posterior transverse commissural sensory canal in Coelacanthids of later geological periods); *fe. com*, fenestra in dermal cranial roof, filled by the large ascending tube of the infraorbital sensory canal; *fe. ena*, part of fenestra endonarina communis representing fenestra endonarina anterior; *fe. enp*, part of fenestra endonarina communis representing fenestra endonarina posterior; *fe. exa*, fenestra the ventral part of the bone further back, laterally to the anterior part of the fossa ventro-lateralis. The presence of these two fine canals (c_1buc, c_2buc) proves that the r. buccalis lateralis must have passed forwards through the lateral part of the fossa ventro-lateralis. It must have entered the fossa through the groove *gr. buc* (figs. 74 B, 76 C; p. 561) in the lower margin of the postnasal wall and must have left it anteriorly through the groove gr_abuc. It is thus evident that the r. buccalis lateralis entered the nasal cavity at the postero-ventral corner of the fenestra endonarina communis. The posterior horizontal part of the lateral rostral in *Nesides* is pierced on its dorsal side by a fairly wide foramen, *f. com. trp* (fig. 77 A), which leads upwards from the infraorbital sensory canal. This foramen may have given passage to a long ascending sensory canal tube (*com. trp*, fig. 32 A) which in Coelacanthids of later geological periods presumably was modified into the posterior transverse commissure between the infraorbital and supraorbital sensory canals (cf. pp. 336, 338, 584).

In the holotype of *Diplocercides kayseri* the medial face of the left lateral rostral is completely preserved and exposed (*R. l*, pl. 16, fig. 2; cf. fig. 77 B, C; Stensiö 1937 a, pl. 1; pl. 10, fig. 1). It consists in the main of a tube-shaped part, bent in a similar way as that in *Nesides*, but has also certain other parts, not shown and probably not preserved in *Nesides*. The foramen *f. com. trp* is developed in a similar way as in *Nesides*. It lies, however, at the bottom of a deep notch in the dorsal margin of the bone. This notch is bounded posteriorly by a thin ascending lamina, the postero-dorsal facial lamina (*la. pd*), and anteriorly by a strong antero-dorsal process (*pr. R. l*), which is truncated dorsally and has a concave anterior margin. The antero-ventral part of the bone in *Diplocercides* is developed as a thin antero-ventral facial lamina (*la. av*), which extends downwards and forwards. The medial side of the bone shows several foramina (*f. R. l*; pl. 16, fig. 2; cf. Stensiö 1937 a, p. 21) which must have been traversed by branches of the r. buccalis lateralis and r. maxillaris V and by vessels (cf. fig. 78 B).

It is very likely that also the lateral rostral in *Nesides* had equivalents to the postero-dorsal and antero-ventral facial laminae and to the antero-dorsal process of the lateral rostral in *Diplocercides* and was thus essentially as in *Diplocercides*. From the very similar way in which the la-

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exonarina anterior; *fe. o*, fenestra orbitalis; fe_1exp, fe_2exp, fenestrae exonarinae posteriores; gr_abuc, anterior groove for r. buccalis lateralis, r. maxillaris V and vessels; *gr. soc*, groove for supraorbital sensory canal ridge; *i. ena*, notch for anterior nasal tube; *i. enp*, notch for posterior nasal tube; *ioc*, infraorbital sensory canal; *i. R. l*, notch for antero-ventral end of lateral rostral; *la. Aup*, ascending lamina of autopalatine; *la. av*, *la. pd*, antero-ventral and postero-dorsal facial laminae of lateral rostral; *pr. R. l*, antero-dorsal process of lateral rostral; *pr. v*, ventral process of postnasal wall.

teral rostral was attached to the endocranium in *Nesides* and *Euporosteus* it may be concluded that also in the latter genus it was on the whole as in *Diplocercides.* If, as thus seems highly probable, the lateral rostral actually was developed very much in the same way in *Euporosteus*, *Nesides* and *Diplocercides*, it had the following position in relation to the endocranium in these three genera (fig. 77 B, C). The tube-shaped part of the bone surrounding the infraorbital sensory canal was intimately attached to the endocranium along the antero-dorso-lateral edge of the postnasal wall and on the protuberance *kn. R. l* and the facet *ar. R. l* of the lateral nasal wall (figs. 73 B, 74, 76). As is clearly shown in *Euporosteus* (p. 567), the foremost portion of the tube-shaped part lay in the lateral part of the groove $gr_{c}ioc$ between the fenestra endonarina communis (*fe. en*, fig. 73) and the ventral rostral process (*pr. rv*, fig. 74 A). The antero-ventral facial lamina (*la. av*) covered the outside of the ledge ventrally to the groove $gr_{c}ioc$ and its antero-ventral end occupied the notch *i. R. l* (figs. 74 A, 77 C) laterally to the ventral rostral process. The antero-ventral end of the lateral rostral thus extended forwards onto the ventral face of the endocranium. Between the protuberance *kn. R. l* and the facet *ar. R. l* it was not attached to the lateral nasal wall but together with the groove $gr_{a}buc$ (figs. 73 B, 76 B) formed a short canal (*c. buc*, fig. 77 B, C) leading forwards and upwards to the nasal cavity. In *Diplocercides* this canal may at least sometimes be bounded by endoskeleton also on its lateral side (cf. pp. 554, 561; *lat. for*). It was beyond doubt traversed by the r. buccalis lateralis, but the presence of several foramina on the medial face of the lateral rostral (*f. R. l*, pl. 16, fig. 2) shows that in this part of its course the r. buccalis was probably accompanied by other nerves or vessels, presumably the r. maxillaris V, the a. maxillaris and the v. infraorbitalis (cf. fig. 78 B; cf. also p. 599). As the most anterior ones of the foramina on the medial face of the lateral rostral are situated above the area attached to the facet *ar. R. l* on the lateral nasal wall, it is obvious that the r. buccalis, r. maxillaris V, a. maxillaris and v. infraorbitalis (fig. 78 B) passed forwards in the ventro-lateral part of the nasal cavity close to the lateral rostral, more precisely close medially to the part of the lateral rostral closing the ventral part of the fenestra endonarina communis. In their further course forwards these nerves and vessels must have left the nasal cavity either in the groove $gr_{c}ioc$ or through the prenasal wall (cf. pp. 263, 578, 600). The postero-dorsal facial lamina of the lateral rostral (*la. pd*) covered a posterior dorsal part of the fenestra endonarina communis and the part of the lateral nasal and postnasal walls that is situated ventrally to the groove *gr. ntp* (fig. 73 B). Finally, the antero-dorsal process of the lateral rostral (*pr. R. l*) had such a position that it divided the upper part of the fenestra endonarina communis into two divisions, anterior and posterior. The anterior division (*fe. ena*, fig. 77 B), which at least in *Euporosteus* is represented by the notch *i. ena* at the anterior dorsal corner of the fenestra endonarina communis (fig. 73 B), transmitted the anterior external nasal tube and is thus a fenestra endonarina anterior. In the exoskeleton just outside was the fenestra exonarina anterior (*fe. exa*, fig. 77 B), which seems to have been small, and was bounded posteriorly and postero-ventrally by the concave anterior margin of the antero-dorsal process of the lateral rostral. Its other boundaries could not be ascertained. The posterior division of the upper part of the fenestra endonarina communis (*fe. enp*, fig. 77 B) was developed for the posterior external nasal tube and is thus a fenestra endonarina posterior. The opening in the exoskeleton outside this division (*fe. com*, fig. 77 B) is not a fenestra exonarina posterior, for it was not traversed by the posterior external nasal tube, which, as will be shown below, passed backwards through a canal in the posterior tectal. It is bounded anteriorly, ventrally and posteriorly by the notch in the dorsal margin of the lateral rostral between the antero dorsal process and the postero-dorsal facial lamina (*la. pd*), and at its bottom lies the opening *f. com. trp* (pl. 16, fig. 2), probably for the strongly developed ascending sensory canal tube (*com. trp*, fig. 32 A), which may correspond to the posterior transverse sensory canal commissure in Coelacanthids of later geological periods (*com. trp*, figs. 32 B, C, 35). As we shall see below it agrees in all respects with the opening *fe. com* in *Latimeria* (fig. 35; p. 588).

The posterior tectal (antorbital of previous descriptions: Stensiö, Nielsen, Moy-Thomas) is fairly completely preserved only on the left side in *Nesides*, where its medial face is exposed (*Te. p*, fig. 77 A; pl. 16, fig. 4; Stensiö 1937 a, p. 7; figs. 2, 3; pl. 10, figs. 2, 3). In *Euporosteus* there is only a fragment preserved on the dorsal face of the postnasal wall (*Te. p*, fig. 77 B; pl. 14; Stensiö 1937 a, fig. 10; pl. 11, fig. 4; pl. 12, fig. 1). The posterior tectal in *Nesides* is roughly triangular in shape and covers the lateral part of the dorsal face of the postnasal wall. It extends somewhat backwards beyond the ethmoidal region, entering into the anterior boundary of the orbital opening (*fe. o*, fig. 77 A). The anterior part of the bone is thickened and pierced by a wide rostro-caudal canal (*c. ntp*, pl. 16, fig. 4) leading backwards from the postero-dorsal corner of the fenestra endonarina communis and passing over into a groove in the medial face of the bone. This groove does not extend backwards to the orbit, but leads to an opening in the posterior tectal (fe_2exp, fig. 77 A; pl. 16, fig. 4). Another somewhat smaller opening leads out from the middle part of the groove (fe_1exp, fig. 77 A; pl. 16, fig. 4). The canal in the anterior part of the posterior tectal and the groove in the posterior continuation of the canal were clearly developed for a duct which passed backwards from the postero-dorsal corner of the fenestra endonarina communis and opened with two apertures on the outside of the posterior tectal. It is quite evident that this duct must have been the posterior external nasal tube (*ntp*, fig. 79). The posterior nasal tube thus bifurcated posteriorly into two branches, an anterior and a posterior one, which opened outwards separately by two openings in the posterior tectal (*fe*$_1$*exp*, *fe*$_2$*exp*) representing two fenestrae exonarinae posteriores. The posterior tectal in *Euporosteus* (fig. 77 B) was presumably developed essentially as that in *Nesides* and we are consequently justified in concluding that the groove *gr.ntp* (fig. 73 B) behind the postero-dorsal part of the fenestra endonarina communis in *Euporosteus* was caused by the thickened anterior part of the posterior tectal containing the canal for the posterior external nasal tube.

There were thus even in these early Coelacanthids, as in *Latimeria* (p. 588), one anterior and two posterior external nostrils on either side.

Our description of the cavities and canals of the snout has to be based mainly on the grinding-series of *Nesides*.

The anterior part of the cranial cavity (*cav.cr*, figs. 75 B, 78 A; cf. fig. 75 A) is but slightly higher than broad and rounded in transverse sections. It is situated comparatively high above the basis cranii and thus has a very thick floor. The roof too is fairly thick, whereas the lateral walls are thin. The cranial cavity passes over into the canales olfactorii about at the transition between the orbitotemporal and ethmoidal regions and thus has no ethmoidal part.

The canalis olfactorius (*c.olf*, figs. 75 B, 76 A, C, 78 A; cf. fig. 79) is fairly long and runs forwards and somewhat laterally and downwards. Its anterior parts are situated strikingly far ventrally, just as in *Latimeria* (fig. 83 B) and are also of a similar shape as in that form. Its very foremost part was not preserved, but beyond doubt the canal opened into the posterior ventro-medial corner of the nasal cavity (cf. p. 564). The canal consists of a posterior long and wide portion (*p.bulb*, fig. 78 A), which housed the bulbus olfactorius, and an anterior narrower and shorter portion (*p.I*), which was traversed by the olfactory nerve. The shape of these two portions in transverse section is shown in figs. 75 B and 76 C.

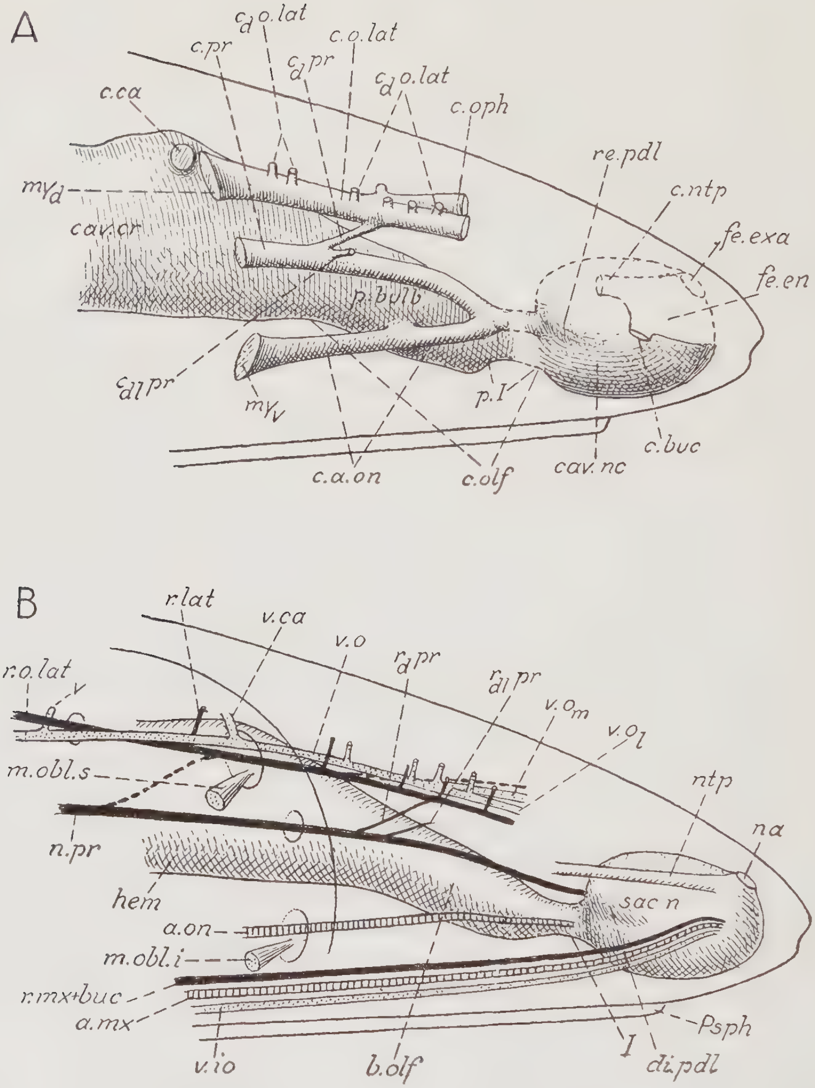
The development of the cranial cavity and olfactory canals in *Nesides* seems to show that the general features of the forebrain and olfactory nerves were very much as follows (figs. 78 B, 79). The hemispheres (*hem*) were long and of a uniform height and width throughout their rostrocaudal extent. They lay close to one another. The bulbi olfactorii (*b.olf*) were long and fairly high and narrow. They lay in front of the hemispheres, but were separated throughout from each other: The n. olfactorius (*I*) was short and lay in the foremost short portion of the olfactory canal.

The nasal cavity is fairly small. In *Nesides* (*cav. nc*, figs. 76 A, C, 78 A) it is about as broad as long at the bottom, but was presumably narrower at the top and has a main chamber and at least two recesses, the antero-medial recess (*re. am*) and the postero-dorso-lateral recess (*re. pdl*). In *Diplocercides* (pl. 16, fig. 3) the nasal cavity is longer and narrower.

The nasal sac in *Nesides* (*sac n*, figs. 78 B, 79) must on the whole have had a shape corresponding to that of the nasal cavity, with a main part and at least two diverticles, the antero-medial diverticle (*di.am*) and the postero-dorso-lateral diverticle (*di. pdl*). From the nasal sac issued the anterior external nasal tube (*nta*, fig. 79) through the antero dorsal part of the fenestra endonarina communis (the notch *i. ena*) and through the fenestra exonarina anterior. Somewhat further back the posterior external nasal tube (*ntp*; figs. 78 B, 79) passed off from the lateral part of the nasal sac. It left the nasal cavity through the posterior dorsal part of the fenestra endonarina communis, traversed the canal (*c. ntp*; p. 579) in the anterior part of the posterior tectal, and then continued backwards between the posterior tectal and the endocranium, dividing into two branches which pierced the posterior tectal independently of one another and opened outwards through two posterior external nostrils (np_1, np_2, fig. 79).

The canal for the n. trochlearis and the canal presumably transmitting a vein from the cranial cavity (*c. IV*, *f. v*, fig. 73 B, 76 B) have been dealt with above (p. 563). From the foremost dorsal part of the cranial cavity a canal (*c. ca*, figs. 75 B, 76 B, 78 A) which must have transmitted the v. cerebralis anterior, goes off outwards through the lateral cranial wall and opens at a somewhat different point in *Nesides* and *Euporosteus* (cf. p. 563).

In *Nesides* the anterior part of the tectum orbitale is pierced by two vertical canals (*c. lat*, figs. 74 B, 76 A) which have their upper orifices in the groove for the supraorbital sensory canal (*gr. soc*). The anterior canal ascends from the groove (*gr. o. lat*, figs. 74 B, 76 B) on the lateral face of the interorbital wall connecting the anterior and posterior canals for the r. ophthalmicus lateralis, whereas the posterior canal issues from the hinder canal ($c_{p}o.$ *lat*) for the r. ophthalmicus lateralis. These canals have thus undoubtedly transmitted branches of the r. ophthalmicus lateralis. Similar canals are also found in the tectum orbitale of *Euporosteus* (STENSIÖ 1937 a; *nc*, fig. 10). Further laterally in the tectum orbitale of that form there are also a few other canals (*c. n. va*, pl. 14, fig. 2),


A
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fe.en
p.bulb
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cav.nc
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m.obl.s
ntp
na
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hem
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a.on
m.obl.i
r.mx+buc
a.mx
Psph
v.io
b.olf
I
di.pdl

Fig. 78. *Nesides schmidti* Stensiö. *A*, casts of the cavities and canals of the snout, with outlines of the anterior parts of the endocranium and parasphenoid. After a model in wax based on a grinding-series through the endocranium. Lateral view. $^6/_1$. *B*, attempted restoration of the forebrain, nasal sac, and main nerves and vessels of the snout based on the model shown in *A*. A. ophthalmica omitted.

Psph, parasphenoid; *a. mx*, a. maxillaris; *a. on*, a. orbitonasalis; *b. olf*, bulbus olfactorius; *c. a. on*, canal, probably for orbitonasal artery; *cav. cr*, cranial cavity; *cav. nc*, nasal cavity; *c. buc*, canal for r. buccalis lateralis, r. maxillaris V and vessels; *c. ca*, canal for v. cerebralis anterior; $c_{dl}pr$, c_dpr, dorso-lateral and dorsal branches of anterior profundus canal; $c_do.\ lat$, ascending branches of the canal *c. o. lat*; *c. ntp*, canal in posterior tectal for posterior nasal tube; *c. o. lat*, anterior canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. oph*, canal for branch of v. ophthalmica; *c. pr*, anterior profundus canal; *di. pdl*, postero-dorso-lateral diverticle of nasal sac; *fe. en*, fenestra endonarina communis;

which were not to be detected in the grinding-series of *Nesides*, and which also ascend into the tectum orbitale. They may have been developed for branches of the n. profundus or for vessels. It could not be established whether they emerge onto the dorsal face of the tectum orbitale.

The anterior canal for the r. ophthalmicus lateralis (*c. o. lat, my. d*, figs. 73 B, 74 B, 75 B, 76 B, C, 78 A; pl. 14, fig. 2), which presumably transmitted also the v. ophthalmica, the a. ophthalmica and branches of n. profundus, differs somewhat in *Euporosteus* and *Nesides* as regards the position and development of its posterior orifice (pp. 562—563). In the hinder parts of the ethmoidal region the canal goes forwards in the endoskeleton ventrally to the groove (*gr. soc*, fig. 76 C) for the supraorbital sensory canal, but it is impossible to determine whether it then ascends to the dorsal face of the ethmoidal region or leads to the nasal cavity. In *Nesides*, where it could be followed forwards to somewhat behind the nasal cavity, a dorsal branch (c_dpr, figs. 76 A, C, 78 A) ascends to it from the profundus canal. About opposite the junction with this ascending branch the anterior canal for the r. ophthalmicus lateralis gives off a strong medial branch (*c. oph*, fig. 78 A) which goes forwards and a little upwards, presumably to the dorsal face of the ethmoidal region. This branch could be followed only a short distance forwards. It gives off a small dorsal branch to the dorsal face of the ethmoidal region medially to the groove (*gr. soc*) for the supraorbital sensory canal (the medial one of the canals $c_do.\,lat$ in fig. 76 C), and was presumably developed for a branch of the v. ophthalmica ($v.\,o_m$, fig. 78 B; pp. 578—579) and probably also for a branch of the n. profundus. In the part preserved the anterior canal for the r. ophthalmicus lateralis gives off numerous fine branches ($c_do.\,lat$) which pass upwards and open in or at the side of the groove (*gr. soc*) for the supraorbital sensory canal. The anterior canal for the r. ophthalmicus lateralis in *Euporosteus* has its posterior orifice much further backwards and its hindmost part was therefore presumably not traversed either by the v. ophthalmica or the a. ophthalmica (see pp. 578—579). The v. ophthalmica in *Euporosteus* may have pierced the lateral wall of the hindmost part of the anterior ophthalmicus

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fe. exa, fenestra exonarina anterior; *hem*, hemisphere of forebrain; *m. obl. i*, m. obliquus inferior; *m. obl. s*, m. obliquus superior; my_d, my_v, dorsal and ventral anterior myodomes; *na*, anterior external nostril; *n. pr*, n. profundus; *ntp*, posterior nasal tube; *p. bulb*, part of canalis olfactorius which probably lodged bulbus olfactorius; *p. I*, part of canalis olfactorius which probably lodged n. olfactorius; *re. pdl*, postero-dorso-lateral recess of nasal cavity; $r_{dl}pr$, r_dpr, dorso-lateral and dorsal profundus branches; *r. lat*, branch of r. ophthalmicus lateralis; *r. mx + buc*, r. buccalis lateralis and r. maxillaris V (truncus infraorbitalis); *r. o. lat*, r. ophthalmicus lateralis; *sac n*, nasal sac; *v*, vein from cranial cavity; *v. ca*, v. cerebralis anterior; *v. io*, v. infraorbitalis; *v. o*, v. ophthalmica; $v.\,o_l$, $v.\,o_m$, lateral and medial branches of v. ophthalmica; *I*, n. olfactorius.

lateralis canal through the foramen *c.v.o* (figs. 73 B, 74 A) to emerge in the anterior dorsomedial corner of the orbit, whereas the a. ophthalmica in this form entered the postnasal wall through the canal *c.a.o*, which probably ascended to the anterior ophthalmicus lateralis canal.

The anterior profundus canal in *Nesides* (*c.pr*, figs. 75 B, 76, 78 A; cf. fig. 79) is long and goes from the orbit forwards and slightly downwards to the nasal cavity, where its anterior orifice is situated somewhat dorso-laterally to the anterior orifice of the canalis olfactorius. It gives off a strong dorsal branch ($c_{d}pr$) to the anterior canal for the r. ophthalmicus lateralis and also a fine dorso-lateral branch ($c_{dl}pr$). Anteriorly it unites with the canal for the orbitonasal artery (*c.a.on*). In *Euporosteus* only the posterior orifice is known of the anterior profundus canal (*c.pr*, figs. 73 B, 74 A, 75 A).

The canal for the orbitonasal artery in *Nesides* (*c.a.on*, figs. 75 B, 76 B, 78 A, 79; cf. pp. 598—599) pierces the ventral part of the postnasal wall. Its hindmost part is widened (my_{v}; cf. p. 561), probably for the origin of the m. obliquus inferior (*m.obl.i*, fig. 78 B). The canal first goes forwards and somewhat medially, passing close to and for a short stretch communicating with the bulbar portion of the canalis olfactorius, after which it turns a little laterally and unites with the foremost part of the anterior profundus canal.

Judging from the canals now described and other conditions discussed above the course of the main nerves and vessels of the snout in *Nesides* and probably also in *Diplocercides* and *Euporosteus* may be assumed to have been somewhat as follows (figs. 78 B, 79).

After leaving the trigemino-facialis ganglionic complex the r. ophthalmicus lateralis (*r.o.lat*) first traversed the posterior ophthalmicus lateralis canal ($c_{p}o.lat$). In front of that it lay in a groove (*gr.o.lat*) in the upper part of the lateral face of the interorbital wall and then entered and traversed the anterior ophthalmicus lateralis canal (*c.o.lat*), which extends at least to the foremost parts of the postnasal wall. The further forward course of the nerve is unknown. The nerve gave off fine dorsal branches to the supraorbital sensory canal through some of the canals $c_{d}o.lat$.

In the orbit the n. profundus (*n.pr*) probably gave off a few weak dorsal branches to the area above the eye and a branch which entered the anterior ophthalmicus lateralis canal through its posterior orifice and continued forwards through the posterior part of this canal and the canal *c.oph*. Twigs of this branch may have traversed some of the posterior canals $c_{d}o.lat$. The n. profundus then passed forwards to the nasal cavity through the anterior profundus canal (*c.pr*). In this canal it sent off a fine dorsal-lateral branch ($r_{dl}pr$) and a comparatively strong

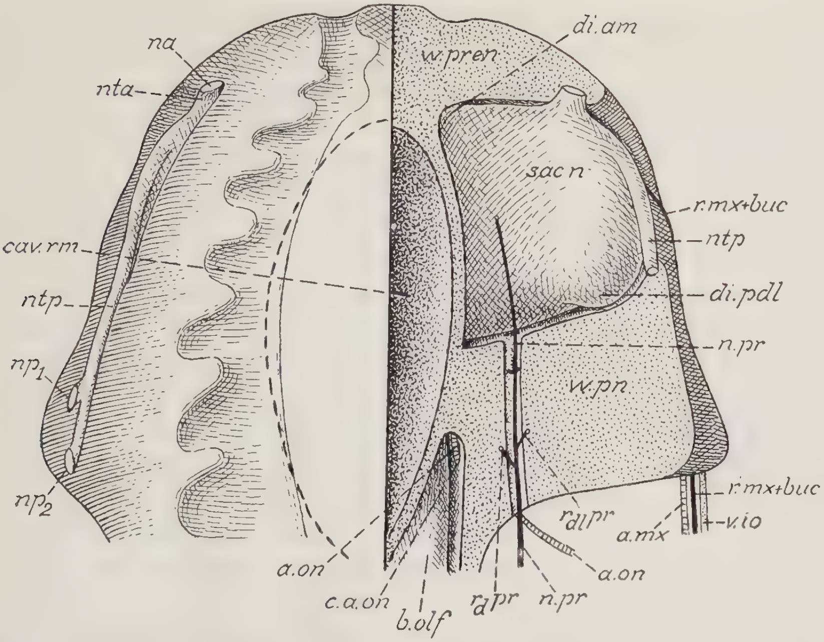

Fig. 79. Attempted restoration of the anterior part of the endocranium of *Euporosteus* in dorsal aspect. On the left side is shown a lateral part of the nasal sac with the anterior and posterior external nasal tubes in their position in relation to the endoskeleton. On the right side the endocranium removed down to the level of the posterior profundus canal. The internal parts on this side restored according to the conditions in *Nesides*. The bulbus olfactorius and certain nerves and vessels shown. The probable extent of the dorsal part of the presumed median rostral cavity indicated on the left side of the figure with broken line. Cartilage dotted. $^7/_1$.

a. mx, maxillary artery; *a. on*, orbitonasal artery; *b. olf*, bulbus olfactorius; *c. a. on*, canal for orbitonasal artery; *cav. rm*, median rostral cavity; *di. am*, antero-medial diverticle of nasal sac; *di. pdl*, postero-dorso-lateral diverticle of nasal sac; *na*, anterior external nostril; *n. pr*, n. profundus; *nta*, *ntp*, anterior and posterior nasal tubes; np_1, np_2, posterior external nostrils; $r_{dl}pr$, $r_d pr$, dorso-lateral and dorsal profundus branches; $r. mx + buc$, r. buccalis lateralis and r. maxillaris V; *sac n*, nasal sac; *v. io*, infraorbital vein; *w. pn*, postnasal wall; *w. pren*, divisio prenasalis communis.

dorsal one ($r_d pr$). The latter ascended through the canal $c_d pr$ to the anterior ophthalmicus lateralis canal, where it accompanied the r. ophthalmicus lateralis, giving off several twigs (through the anterior canals $c_{a}o. lat$) to the overlying dermal bones and the skin. Though it entered the nasal cavity fairly low down, the n. profundus must nevertheless have passed dorsally to the nasal sac. Its further course in the nasal cavity and in the rostral part of the snout is unknown. As the r. maxillaris V presumably was well developed and extended forwards at least into the ventro-lateral part of the nasal cavity, the n. profundus probably did not take part to any great extent in the innervation of the lateral parts of the snout.

The r. buccalis lateralis, which together with the r. maxillaris V probably formed a truncus infraorbitalis (*r. mx + buc*, figs. 78 B, 79), was conceivably accompanied by an artery, the a. maxillaris (*a. mx*), and a vein, the v. infraorbitalis (*v. io*). It passed forwards through the anterior ventro-lateral part of the orbit and then through a groove (*gr. buc*, figs. 73 B, 74, 75 A, 76 C) in the lower margin of the postnasal wall to the fossa ventro-lateralis (*fo. vl*). Here it lay laterally to the ascending lamina (*la. Aup*, fig. 77 B) of the autopalatine ossification and medially to the foremost part of the lachrymojugal and the posterior part of the lateral rostral. From the ventrolateral fossa it went forwards and somewhat upwards to the nasal cavity (in *Nesides* and *Euporosteus* through the groove $gr_{a}buc$ and the canal *c. buc*; in *Diplocercides* through the canal *lat. for*). Within the nasal cavity it passed forwards close medially to the lower margin of the fenestra endonarina communis and medially to the lateral rostral. Its course in front of the nasal cavity could not be established. It may either have pierced the prenasal wall or have continued in the groove $gr_{e}ioc$ occupied by the anterior portion of the tube-shaped part of the lateral rostral surrounding the infraorbital sensory canal. During its passage in the snout the truncus infraorbitalis and the vessels accompanying it gave off several branches, inter alia to the lateral rostral.

The r. palatinus VII must have passed forwards ventrally to the ethmoidal region but otherwise nothing can be said of its course (cf. pp. 599—600.

The presumed orbitonasal artery (*a. on*, figs. 78 B, 79) must have run forwards dorsally to the m. obliquus inferior (*m. obl. i*), then entering the canal *c. a. on* (figs. 78 A, 79) in the lower part of the postnasal wall. Through this it reached the olfactory canal, in which it probably continued forwards to the nasal cavity (cf. *Polypterus*, p. 263, fig. 9; cf. also pp. 598—599).

Besides the arteries mentioned (*a. mx*, *a. on*) there was probably also an a. ophthalmica in the snout, accompanying the r. ophthalmicus lateralis forwards from the orbit (cf. *Polypterus*, p. 263, fig. 9). In *Nesides* it seems to have entered the anterior ophthalmicus lateralis canal through the orbital orifice. In *Euporosteus*, on the other hand, it seems to have left the orbit close medially to the n. profundus through the canal *c. a. o* (fig. 73 B), in which it then ascended to the anterior ophthalmicus lateralis canal.

The snout seems to have been drained at least by two veins, a ventral one, the v. infraorbitalis (*v. io*, figs. 78 B, 79), which accompanied the truncus infraorbitalis (see above), and a dorsal one, the v. ophthalmica (*v. o*, fig. 78 B). The latter was probably formed by the confluence of two large branches, lateral and medial. The medial branch ($v.\,o_m$) received the blood from the anterior dorso-medial parts of the snout and went backwards through the canal *c. oph* (fig. 78 A) to the anterior ophthalmicus lateralis canal. Here it joined the lateral branch ($v.\,o_l$), which presumably drained certain antero-lateral parts of the snout and possibly had a tributary from the nasal cavity. After the union of the two main branches the vein went backwards to the orbit through the anterior ophthalmicus lateralis canal, receiving tributaries through some of the canals $c_a o.\,lat$ (fig. 78 A) and emerging in the orbit through or somewhat in front of the orbital orifice of the anterior ophthalmicus lateralis canal (in *Euporosteus* through the canal *c. v. o*, figs. 73 B, 75 A). On entering the orbit it passed dorsally to the m. obliquus superior (*m. obl. s*) and there received the v. cerebralis anterior (*v. ca*) from the cranial cavity. Further back in the orbit also a second vein (*v*, fig. 78 B) coming from the cranial cavity together with or close to the n. trochlearis emptied into the v. ophthalmica.

It is not impossible that there also existed an orbitonasal vein (cf. p. 598), which left the nasal cavity through the profundus canal (*c. pr*) and then from the foremost part of that canal continued backwards to the orbit through the canal *c. a. on* accompanying the a. orbitonasalis in the hinder part of that canal.

b. **Dictyonosteus arcticus Stensiö.**

(Pl. 17.)

Dictyonosteus arcticus from the Upper Middle Devonian of Spitzbergen (Fish Cleft, Mimer Valley; Säve-Söderbergh 1932, pp. 32—33; 1934 a, p. 50; 1937, pp. 30, 37; Heintz 1937, p. 19; Nilsson 1941, pp. 42—51; Høeg 1942, pp. 161—170) was long regarded by Stensiö as a Rhipidistid Crossopterygian (Stensiö 1918; 1921, pp. 131—134, fig. 58; 1922 a, pp. 1241—1249, figs. 1—3; pl. 1, figs. 1—4; 1925, pp. 65—68, fig. 13; Holmgren and Stensiö 1936, pp. 345—359; figs. 265, 272 B). A later investigation carried out by him (Stensiö 1937 a, p. 32) has shown, however, that as regards the development of the fronto-ethmoidal shield and the course of the supraorbital sensory canal *Dictyonosteus* reminds decidedly of the Coelacanthids. "As far as may be judged therefore", Stensiö says, "it is likely that *Dictyonosteus* in some way is fairly closely related to the ancestors of the Coelacanthids." My investigation of the holotype of *Dictyonosteus* confirms the impression of a close connection with the later Devonian Coelacanthids. As regards the snout, *Dictyonosteus* in fact agrees with the Coelacanthids, while it differs fundamentally from both *Porolepiformes* and *Osteolepiformes*. In these circumstances we may now be justified definitely to refer *Dictyonosteus* to the Coelacanthids. As it is undoubtedly the oldest representative of the Coelacanthids known with certainty at present, it is of great interest from all points of view.

For his investigations referred to above STENSIÖ made certain preparations of the holotype of *Dictyonosteus*, which exposed inter alia the foremost part of the supraorbital sensory canal of the left side. This part of the supraorbital sensory canal lies fairly close to the median line of the snout, about as the corresponding part of the supraorbital sensory canal in other Coelacanthids (fig. 32 A; cf. *gr. soc*, fig. 73 A), and pierces the dermal bone that STENSIÖ in 1921 (fig. 58) regarded as the interrostral. This condition and several others pointed out to me by STENSIÖ show that his restoration (STENSIÖ 1921, fig. 58; HOLMGREN and STENSIÖ 1936, fig. 272 B) of the dermal bones and sensory canals of the snout in *Dictyonosteus* is incorrect in several important respects. The "interrostral" of this restoration must actually be a nasal, in all probability the foremost element in the nasal series. It is thus a paired bone. The three bones interpreted by STENSIÖ as "nasals" do not appear to be pierced by the supraorbital sensory canal, but lie laterally to that canal. The foremost one lies laterally to the foremost nasal element now identified and is situated on the tectum nasi, as are the other two "nasals". We must conclude, therefore, that these three bones are tectals (*Te. a*, pl. 17, fig. 2; cf. fig. 35; p. 351).

The supraorbital sensory canal is narrow throughout its extent, much narrower than in other Coelacanthids, which presumably is a primitive condition (cf. p. 339). Throughout the larger posterior part of its course it has, as pointed out by STENSIÖ (1937 a, p. 32), a more or less decided sutural (interosseal) position (cf. STENSIÖ 1921, fig. 58; the course of the canal in the lateral part of the frontal). It is therefore remarkable that it pierces at least the foremost nasal element of the snout.

The ethmoidal region (pl. 17) is badly crushed and damaged. Several parts are even so poorly preserved, that nothing at all can be said concerning their development.

Preparations of the endocranium now made reveal that the statement by STENSIÖ (1922 a, p. 1242; 1932, p. 18; HOLMGREN and STENSIÖ 1936, p. 345) that the ethmoidal region in *Dictyonosteus* is occupied by a paired ossification separated from the ossification in the orbitotemporal region is not correct. In fact there is in *Dictyonosteus*, as in *Diplocercides*, *Nesides*, *Euporosteus*, *Porolepiformes* and *Osteolepiformes*, a large continuous ethmosphenoid (*Etsph*, pl. 17, figs. 1, 2), which occupies both the orbitotemporal and ethmoidal regions.

The ethmoidal part of the ethmosphenoid is much more strongly ossified in *Dictyonosteus* than in *Diplocercides*, *Nesides* and *Euporosteus*, and is made up not only of perichondral bone but also to a large extent of cancellated enchondral bone. It is obvious, however, that the internasal wall to a large extent consisted of cartilage.

The lower side of the anterior part of the endocranium (pl. 17, fig. 1) is very much as in other Devonian Coelacanthids (cf. fig. 74). The parasphenoid (*Psph*) is broad and at either side of its anterior end there is a depressed area (*ar. Vo*) which is essentially as the vomeral area in *Euporosteus*. Postero-laterally on either ventro-lateral part of the postnasal wall (*w. pn*) lies a large fossa directed ventro-laterally (*fo. vl*, pl. 17, figs. 1, 2) and obviously corresponding to the fossa ventro-lateralis in *Diplocercides*, *Nesides* and *Euporosteus* (figs. 73 B, 74, 76 B). As in other Devonian Coelacanthids there is no fenestra endochoanalis and no opening whatever leading down to the mouth cavity from the nasal cavity. The "inner nostril" of Stensiö's descriptions (*fe. en*, pl. 17, figs. 1, 2; cf. Stensiö 1918, p. 120; *X*, pl. 5, fig. 1; 1922 a, pp. 1247—1248) has turned out to resemble the fenestra endonarina communis in *Nesides* and *Euporosteus* (cf. figs. 73 B, 76 B) and must be either such a fenestra or a fenestra endonarina anterior. In fact it differs from the fenestra endonarina communis in *Nesides* and *Euporosteus* only by its smaller size.

The posterior face of the postnasal wall (pl. 17, fig. 2) is badly crushed and imperfect, but it is clearly seen that it is devoid of an olfactory ridge, just as in *Diplocercides*, *Nesides* and *Euporosteus*. Like those three forms *Dictyonosteus* also lacks an olfactory ridge on the interorbital wall (cf. figs. 73 B, 74, 75, 76 B; cf. also *Porolepis* and *Eusthenopteron*, *ri. olf*, figs. 37, 47, 49, 50).

The internasal wall is comparatively broad, and as already pointed out, consisted to a large extent of cartilage. It was developed in such a way that it may very well have lodged a median rostral cavity (*cav. rm*, pl. 17, fig. 3) corresponding to that in *Latimeria* (p. 583; figs. 82, 83; cf. fig. 79). The postnasal wall (*w. pn*, pl. 17, figs. 1, 2, 4) is comparatively thick and strongly developed, but it is not so thick as in *Nesides* or *Euporosteus*. The prenasal wall, the tectum nasi and the solum nasi are also well developed and somewhat thicker than the corresponding walls in *Nesides* and *Euporosteus*. Owing to the relatively small size of the fenestra endonarina communis the lateral nasal wall is more complete than in the two forms just referred to.

The nasal cavities (*cav. nc*, pl. 17, figs. 3, 4) lie rather far apart and are fairly small, definitely smaller than in *Nesides* and *Euporosteus*. In the anterior ventro-medial part of the nasal cavity is an antero-medial recess (*re. am*, pl. 17, fig. 3) as in *Nesides* (fig. 76 A).

The foremost part of the cranial cavity is imperfectly known but it is obvious that it lay approximately as in *Nesides* (cf. Stensiö 1922 a, fig. 2). Its floor is high and narrow, however, and most similar to that in *Eusthenopteron* (fig. 49). The canalis olfactorius goes forwards and downwards as in *Nesides* but opens into the nasal cavity (*c. olf.* pl. 17, fig. 3) higher up than in that form and presumably also than in *Latimeria*. In this respect *Dictyonosteus* is probably more primitive than the geologically younger Coelacanthids.

From the orbit several canals lead forwards into the ethmoidal region but owing to the crushed condition of the postnasal wall these canals are difficult to follow. It is fully evident, however, that the main ones are very much as in *Nesides* and *Euporosteus*. In the ventral part of the posterior face of the postnasal wall we thus find a deep pit (*c. a. on*, my_v, pl. 17, figs. 2, 3) which beyond doubt corresponds to the widened hindmost part of the canal for the orbitonasal artery in *Nesides* and *Euporosteus* (cf. figs. 73 B, 75, 76 B). The upper part of that pit (*c. a. on*) was traversed by the orbitonasal artery, whereas the lower part (my_v) served as a place of origin of the m. obliquus inferior. In the anterior dorso-medial corner of the orbit close below the tectum orbitale (*te. o*) is the wide posterior opening of a canal ($my_a + o. lat$, pl. 17, figs. 2, 4), obviously comparable to the widened posterior orifice of the anterior ophthalmicus lateralis canal in *Nesides* (figs. 75 B, 76 B). There are also other canals in the postnasal wall but the interpretation of these is very difficult and I shall not enter upon them here. In this connection it should be added that in *Dictyonosteus* there is also, as in *Diplocercides*, *Nesides* and *Euporosteus*, a posterior profundus canal (Stensiö 1922 a, pp. 1245—1246).

What has now been said proves beyond doubt that *Dictyonosteus* is a Coelacanthid. As might be expected from its geological occurrence it is in certain respects more primitive than the Upper Devonian forms *Diplocercides*, *Nesides* and *Euporosteus*.

c. Remarks on Postdevonian fossil Coelacanthids.

In the Postdevonian fossil Coelacanthids the ossification of the ethmoidal region has undergone a considerable regressive development; the region consisted almost entirely of cartilage, and its morphology is therefore incompletely known (Stensiö 1921; 1922, pp. 198—202; 1932, pp. 30, 51; Watson 1921; Aldinger 1930; Moy-Thomas and Westoll 1935; Nielsen 1936; Moy-Thomas 1937; Holmgren and Stensiö 1936).

Already in the Carboniferous (*Rhabdoderma*; Moy-Thomas 1937, p. 388) and Permian (*Coelacanthus*; Moy-Thomas and Westoll 1935, p. 451) forms there persists of the ethmoidal part of the ethmosphenoid of the Devonian forms only a paired postero-latero-ventral ethmoidal ossification ("ectethmoid"), and no details are known of this ossification in any of the Palaeozoic forms. Also in the Mesozoic forms the ethmoidal part of the ethmosphenoid is represented by a paired ethmoidal ossification only. In *Wimania* (Stensiö 1921, p. 61, figs. 19, 23), *Axelia* (Stensiö 1921, pp. 93—94, figs. 39, 42; pls. 12, 13; pl. 16, fig. 1), *Undina* (Aldinger 1930, pp. 32—33, figs. 1, 4, 5, 6), and *Macropoma* (Watson 1921, pp. 326—327, figs. 4, 5) the posterior part of the lower face of this paired ossification is covered by the antero-lateral part of the parasphenoid. The ossification occupied chiefly the ventral and ventro-lateral parts of the postnasal wall, but at least in *Axelia*, *Undina*, and *Macropoma* it is clearly seen that it extends somewhat forwards inte the solum nasi and somewhat upwards into the lateral nasal wall. In *Macropoma* the vomer lies on the lower side of the ossification, in front of the parasphenoid, its shape and position being very much as those of the vomeral area in *Euporosteus* and *Dictyonosteus* (*ar. Vo*, fig. 74 A; pl. 17, fig. 1). On the lateral face of the ethmoidal ossification *Axelia*, *Undina*, and *Macropoma* have a fossa or wide groove, evidently corresponding to the fossa ventrolateralis in the Devonian Coelacanthids (*fo. vl*, figs. 73 B, 74, 76 B; p. 560), and in front of that fossa or groove there is in *Axelia* and *Undina* a small foramen which undoubtedly corresponds to the canal for the r. buccalis lateralis in *Diplocercides* (*lat. for*; p. 561), *Nesides* and *Euporosteus* (*c. buc*, fig. 77; cf. Stensiö 1921, figs. 39, 42). In *Axelia*, *Undina*, and *Macropoma* a fine canal pierces the foremost part of the ethmoidal ossification from the lower face upwards, probably running to the nasal cavity. This canal seems to be situated somewhat further backwards and medially in *Axelia* than in *Undina* and *Macropoma*. According to Stensiö (1921, pp. 94, 122) it was traversed by a dorsal branch of the r. palatinus VII (cf. *c. palt*, fig. 10 C in *Amia*). In the unnamed Triassic form from East Greenland preliminarily described by Nielsen (1936, pp. 32—33, figs. 14, 15; cf. pp. 336—338) the anterior part of the paired ethmoidal ossification is well exposed (*Et. oss*, fig. 80; *Ecth*, fig. 81) and consists of a ventral horizontal lamina forming the solum nasi (fig. 81) and a lateral vertical lamina forming the lateral nasal wall (*w. l*, fig. 80). Like the lateral nasal wall in *Euporosteus* and *Nesides* (figs. 73 B, 76 B) the vertical lamina is composed of a high posterior division bounding the fenestra endonarina communis posteriorly, and a low anterior division forming the ventral boundary of that fenestra.

Among the Postdevonian fossil Coelacanthids the lateral rostral is fairly well preserved only in the unnamed Triassic form from East Greenland referred to above (*R. l*, figs 80, 81; cf. Nielsen 1936, p. 19; figs. 8—10, 14, 15) and in *Macropoma* (Huxley 1866, pl. 7, fig. 4 ;Watson 1921, fig. 5). In both these forms it is fundamentally as in *Diplocercides*, *Nesides* and *Euporosteus* (cf. fig. 77; pp. 567—571). It is

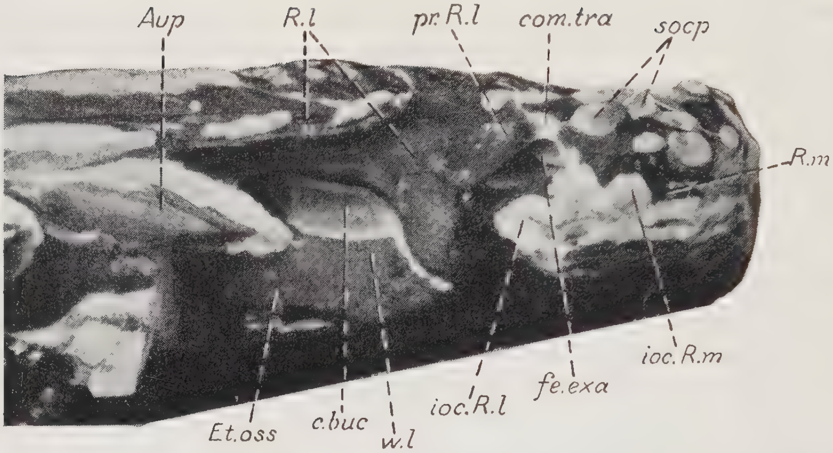

Fig. 80. Undetermined Coelacanthid from the Triassic of East Greenland. Snout seen from the right side with the premaxillary removed. Specimen figured and preliminarily described by NIELSEN (1936, fig. 14). $^4/_1$.

Aup, autopalatine; *Et. oss*, ethmoidal ossification; *R. l*, lateral rostral; *R. m*, medial rostral; *c. buc*, canal for r. buccalis lateralis, r. maxillaris V and vessels; *com. tra*, ventrally directed tube of the longitudinal commissural sensory canal corresponding to the anterior transverse commissural canal in *Latimeria*; *fe. exa*, fenestra exonarina anterior; *ioc. R. l*, *ioc. R. m*, parts of the infraorbital sensory canal enclosed in the lateral and medial rostral resp.; *pr. R. l*, antero-dorsal process of lateral rostral; *socp*, pores of supraorbital sensory canal; *w. l*, lateral nasal wall (low anterior division).

best known in the unnamed Triassic form from East Greenland. Here the lateral rostral (*R. l*, figs. 80, 81) consists of two parts, a tube-shaped one developed around the infraorbital sensory canal (*ioc. R. l*) and an antero-dorsal process (*pr. R. l*). The anterior half of the tube-shaped part is bent down so that its foremost portion extends down to the ventral face of the ethmoidal ossification (*Et. oss*, fig. 80; *Ecth*, fig. 81; cf. fig. 77 C). The position of the bone in relation to the endocranium and the fenestra endonarina communis is fundamentally as in *Nesides* and *Euporosteus* (cf. fig. 77). The canal for the r. buccalis lateralis, r. maxillaris V (truncus infraorbitalis) and vessels (*c. buc*, fig. 80; *nai*, fig. 81) is developed in the same way as in the Devonian forms but is much wider. The antero-dorsal process (*pr. R. l*) is broad and powerful. Immediately behind it lies the posterior transverse commissure between the infraorbital and supraorbital sensory canals (cf. p. 338; *com. trp*, fig. 32 B). This commissure thus agrees in position with the excessively developed dorsal tube (*com. trp*, fig. 32 A) of the infraorbital sensory canal in *Diplocercides* and *Nesides*, which presumably emerged through the opening *f. com. trp* (fig. 77 A; pl. 16, fig. 2; p. 569) in the dorsal border of the lateral rostral. Along the anterior margin of the outer face of the antero-dorsal process in the unnamed Triassic form a groove passes downwards and somewhat backwards (cf. Nielsen 1936, *v. b*, figs. 9, 14) and ends blindly. It housed a ventro-lateral tube of the supraorbital sensory canal (*com. tra*, figs. 32 B, 80) corresponding to the anterior transverse sensory canal commissure of the snout in *Latimeria* (cf. fig. 32 C; pp. 338—339). Immediately in front of and below that tube and just in front of the antero-ventrally facing anterior margin of the antero-dorsal process is an opening that leads inwards to the nasal cavity, a fenestra exonarina anterior (*fe. exa*, fig. 80), situated exactly as in *Diplocercides* and *Euporosteus* (*fe. exa*, fig. 77 B; p. 571).

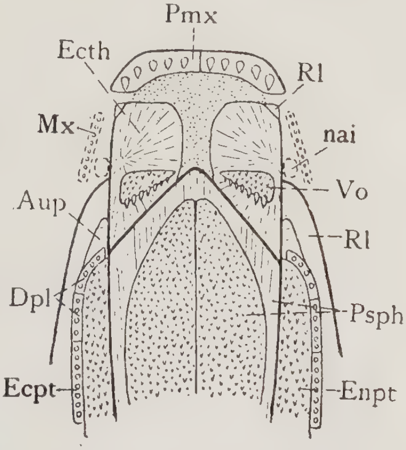

Fig. 81. Diagram showing the anterior parts of the divisio cranialis anterior and palatoquadrate complex in ventral view. This diagram based on the unnamed Coelacanthid reproduced in fig. 80. From Nielsen (1936, fig. 15).

Aup, autopalatine; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Ecth*, ethmoidal ossification; *Enpt*, entopterygoid; *Mx*, tooth plate, probably belonging to the lower jaw (interpreted by Nielsen as the maxillary); *Pmx*, premaxillary; *Psph*, parasphenoid; *R. l*, lateral rostral; *Vo*, vomer; *nai*, the approximate position of the canal (*c. buc*) for the r. buccalis lateralis, etc. (interpreted by Nielsen as the "internal nasal opening").

The posterior tectal in the unnamed Triassic form ("antorbital"; Nielsen 1936, pp. 19, 31—33, figs. 8—10) greatly resembles that in *Nesides* (*Te. p*, fig. 77 A; p. 571). Like that bone it is pierced by two fenestrae exonarinae posteriores, but the anterior one of these is situated in the very ventro-lateral margin of the bone so that it probably consists of a notch only. Two fenestrae exonarinae posteriores are also found in the posterior tectal of several other Postdevonian Coelacanthids (*Axelia*, Stensiö 1921, p. 97; figs. 39, 40, 43, 44; *Whiteia*, Nielsen 1936, figs. 11, 12; Moy-Thomas 1937, fig. 2).

d. Remarks on Latimeria Smith.

(Figs. 32 C, 35, 82, 83.)

The recent Coelacanthid *Latimeria* discovered in 1938 has been described in detail by J. L. B. Smith (1939). The subsequent brief account of the main features of the snout in this form is based on Smith's figures and descriptions. The sensory canals and dermal bones are treated above in a special chapter (pp. 338—339, 346—353).

The snout in *Latimeria* agrees on the whole very well with the snout of fossil Coelacanthids. As in the Postdevonian Coelacanthids the ethmoidal region consists entirely of cartilage except for a paired ethmoidal ossification (*Et. oss*, *38*, figs. 82, 83; "ectethmoid", Smith 1939, pp. 78—80), which has the same position in the region as in Postdevonian Coelacanthids. That it cannot be part of the "palato-pterygo-quadrate system", as maintained by Smith, is so obvious that it needs no explanation. The bone is composed of three portions, an almost horizontal ventral portion (the "fan-shaped base" of Smith's description), which forms the solum nasi, a posterior transverse portion, termed by Smith the "subvertical flange" (*fl. sbv*, fig. 83), which is an almost transverse lamina ascending from the postero-lateral part of the ventral portion and forming the ventro-lateral part of the posterior wall of the nasal cavity, and a lateral columnar portion (the "column" of Smith's description; *col*, figs. 82, 83), which constitutes the lateral boundary of the nasal cavity and corresponds to the high posterior division of the lateral nasal wall in Devonian Coelacanthids (cf. figs. 73 B; 76 B; p. 564). On the lateral face of the lateral columnar portion is a small protuberance (*kn. R. l*, fig. 82) against which rests the lateral rostral. The protuberance is beyond doubt the true equivalent of the correspondingly situated protuberance in Devonian Coelacanthids (*kn. R. l*, figs. 73 B, 76 B; p. 564), which is also developed for the attachment of the lateral rostral. The posterior transverse portion, the "subvertical flange" (*fl. sbv*, fig. 83), seems to correspond to that part of the ethmosphenoid in *Euporosteus* (p. 560; figs. 73 B, 74 A) that forms the antero-medial boundary of the fossa ventro-lateralis and separates that fossa from the nasal cavity. In front of the ventral part of the columnar portion there is a notch in the lateral part of the ventral horizontal portion of the ethmoidal ossification, in which the lateral rostral ("latero-rostro-nasal", Smith) is attached. This notch corresponds to the area *ar. R. l* in Devonian Coelacanthids (figs. 73, 76). Smith says (1939, p. 79) that it lies "above the base", which probably means that it lies on a lateral raised part of the ventral horizontal portion, the "fan-shaped base", of the bone. If this is so, the ventral portion of the bone in front of the columnar portion is provided along its lateral margin with a low dorsal ridge, which corresponds to the low anterior division of the lateral nasal wall in Devonian Coelachanthids. On the postero-lateral corner of the lower face of the ethmoidal ossification, and thus on the lower side of the part of the ethmoidal ossification that bears the columnar portion, lies the articular area of the autopalatine. This area agrees in position with the foremost and somewhat broadened part of the articular facet $art_a aup$ in *Euporosteus* (fig. 74; p. 561).

The internasal wall, the divisio prenasalis communis, the postnasal wall, the tectum nasi, and the anterior part of the interorbital wall are made up of cartilage exclusively or, as regards the postnasal wall, almost exclusively.

The internasal wall is comparatively narrow ventrally, but increases rapidly in breadth in a dorsal direction (fig. 83 B). It houses a large median unpaired cavity, the median rostral cavity (*cav. rm*, *R*, figs. 82, 83; "ethmoidal nasal cavity", SMITH 1939, pp. 54—56, fig. 15), which, however, also extends backwards behind the internasal wall and thus consists of two divisions, internasal and postnasal, the latter lying above the olfactory canals and the foremost part of the cranial cavity. The median rostral cavity is separated completely, though only by thin walls, from the nasal cavities. It is likewise separated from the dermal bones on the dorsal face of the ethmoidal region by a thin endoskeletal wall only. It is deepest in the internasal division and decreases gradually in depth backwards through a raising of the floor. As regards its position the median rostral cavity greatly reminds of the cavum precerebrale in sharks (*cav. prec*, fig. 3, p. 251), and, as that, it seems to represent the embryonic ethmoidal cavity in Gnathostomes in general, which is originally occupied by the foremost part of the brain. That it has something to do "with the medio-dorsal olfactory system in Cyclostomes", as maintained by SMITH (1939, p. 55), is of course quite out of the question, for in *Latimeria*, as in fossil Coelacanthids, there are paired nasal cavities of the ordinary Gnathostome type, which together correspond to the unpaired nasal cavity in Cyclostomes.

The postnasal wall in *Latimeria* is still imperfectly known. As far as can be seen, however, it has no ventro-lateral fossa and seems in fact to be devoid of the postero-lateral part that in Devonian Coelacanthids bears that fossa (*fo. vl*, figs. 73 B, 74, 76 B). Owing to this the ethmoidal region in *Latimeria* is broadest approximately at a transverse plane across the protuberance (*kn. R. l*) of the columnar portion of the ethmoidal ossification and not at a transverse plane through the hinder part of the postnasal wall, as is the case in *Nesides* and *Euporosteus* (figs. 73 A, 74, 76 A).

The anterior part of the cranial cavity and the olfactory canals (*c. olf*, *L*, fig. 83 B; cf. SMITH 1939, p. 91; figs. 15, 16) are almost exactly as in *Nesides* (figs. 75 B, 76 C, 78 A; p. 572). Each olfactory canal, which posteriorly houses the bulbus olfactorius and anteriorly the olfactory nerve, goes forwards and downwards ventrally to the lateral part of the postnasal division of the median rostral cavity and opens into the postero-medial corner of the nasal cavity. The anterior part of this canal thus has a similar basal position as in *Nesides*.

The nasal cavity (*cav. nc*, *E*, figs. 82, 83; SMITH 1939, pp. 56—57) is developed in the same way as in fossil Coelacanthids (cf. figs. 73, 76, 78 A, 79, 80; p. 573) and opens outwards only through a large fenestra endonarina communis (*fe. en*, fig. 82). There is thus no fenestra endochoanalis. The shape and position of the fenestra endonarina communis are essentially as in *Euporosteus* and *Nesides* (cf. figs. 73 B, 76 B), and as in the fossil Coelacanthids it is to a large extent closed on the outside by the lateral rostral. Both in shape and as regards the way in which it is attached to the ethmoidal region this dermal bone (*R. l*, *18*, fig. 35; SMITH 1939, p. 39) agrees fundamentally with that in the fossil Coelacanthids (cf. figs. 77, 80; pp. 567—571, 584). Behind the antero-dorsal process (*pr. R. l*, fig. 35) it has a deep notch in its upper margin. This notch, which lies just outside the postero-dorsal part of the fenestra endonarina communis, is bounded above by the hinder one of the anterior tectals (*Te. a*, fig. 35). The opening in the exoskeleton, thus formed, *fe. com*, transmits the posterior transverse commissure (*com. trp*, figs. 32 C, 35) between the supraorbital and infraorbital sensory canals and corresponds to the opening *fe. com* in Devonian Coelacanthids (fig. 77 B; p. 571). According to SMITH (1939, p. 57) a "tubular" rostro-caudal structure, suspected by him to be an artery, passes through that opening[1]. Between the two places at which the lateral rostral is attached to the ethmoidal ossification (the protuberance *kn. R. l* and the notch in front of the ventral part of the columnar portion) there is an opening between the lateral rostral and the ethmoidal ossification. This opening leads to the nasal cavity at the postero-ventral corner of the fenestra endonarina communis and is thus evidently the exact equivalent of the canal *c. buc* in fossil Coelacanthids (figs. 77, 80; pp. 567, 570, 584). It is about the same size as in the unnamed Triassic form from East Greenland preliminarily described by NIELSEN (fig. 80). It is not known whether in *Latimeria* it is traversed by any nerves and vessels. In the fossil forms it is assumed (figs. 78 B, 79; pp. 570, 578) to have given passage to the r. maxillaris V, the r. buccalis lateralis, the a. maxillaris and the v. infraorbitalis[2].

In *Latimeria* there are three paired external nostrils, one anterior (*na*, figs. 35, 83 A) and two posterior (np_1, np_2, figs. 35, 83 A; cf. *B*, *C*, fig. 82 and SMITH 1939, figs. 5, 11; pls. 11, 12). These three nostrils are undoubtedly homologous to the three nostrils in fossil Coelacanthids, which certainly lay just outside their exonarinal fenestrae (*fe. exa*, fe_1exp,

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[1] It is not impossible that this "tubular structure" is actually the posterior external nasal tube, which at least in the Devonian forms beyond doubt left the nasal cavity at this place and passed backwards just above the posterior part of the tube-shaped portion of the lateral rostral.

[2] SMITH's supposition (1939, p. 103) that the r. buccalis lateralis passes forwards together with the r. palatinus VII through what he describes as the "palatine canal" (*W*, fig. 83 B) cannot possibly be true.

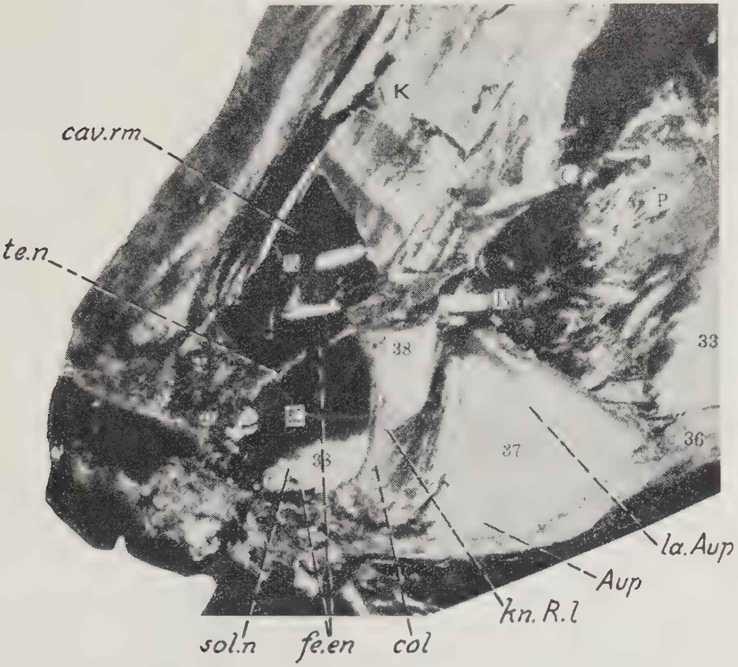

Fig. 82. *Latimeria chalumnae* Smith. Left side of the snout in antero-dorso-lateral view. Certain parts removed to show the median rostral cavity (*R*), the left nasal cavity (*E*), and the anterior part of the palatoquadrate complex. From J. L. B. SMITH (1939, pl. 22). Approx. $^1/_2$.

Aup, autopalatine; *cav. rm,* median rostral cavity; *col,* columnar portion of ethmoidal ossification (the high posterior portion of the lateral nasal wall); *fe. en,* fenestra endonarina communis; *kn. R. l,* protuberance for attachment of lateral rostral; *la. Aup,* ascending lamina of autopalatine; *sol. n,* ventral horizontal portion (the "fan-shaped base") of the ethmoidal ossification forming the solum nasi and perhaps the low anterior division of the lateral nasal wall; *te. n,* wall separating the median rostral cavity from the nasal cavity.

Explanations of the letterings of SMITH with the terms and interpretations given by him.

B, C, lower and upper lateral narial aperture and tube; *E,* olfactory capsule; *K,* cartilage; *P,* muscle; *R,* ethmoidal nasal cavity; *33,* pterygoid; *36,* ectopterygoid; *37,* autopalatine; *38,* ectethmoid.

fe$_2$*exp*, figs. 77, 80; pp. 571—572, 585). The position of the external nostrils in relation to the dermal bones shows, however, certain differences between *Latimeria* and the fossil Coelacanthids. In the fossil forms the anterior external nostril lay immediately in front of the antero-dorsal process of the lateral rostral dorsally to the anterior part of the tube-like sensory-canal-bearing part of that bone and immediately laterally to the antero-dorsal corner of the fenestra endonarina communis (*i. ena*, figs. 73 B, 77 B). In *Latimeria*, on the other hand, the anterior external nostril (*na*$_1$, fig. 35) is situated further anteriorly between the two lateral ones of the three medial rostrals (*R. m*), which certainly is a secondary

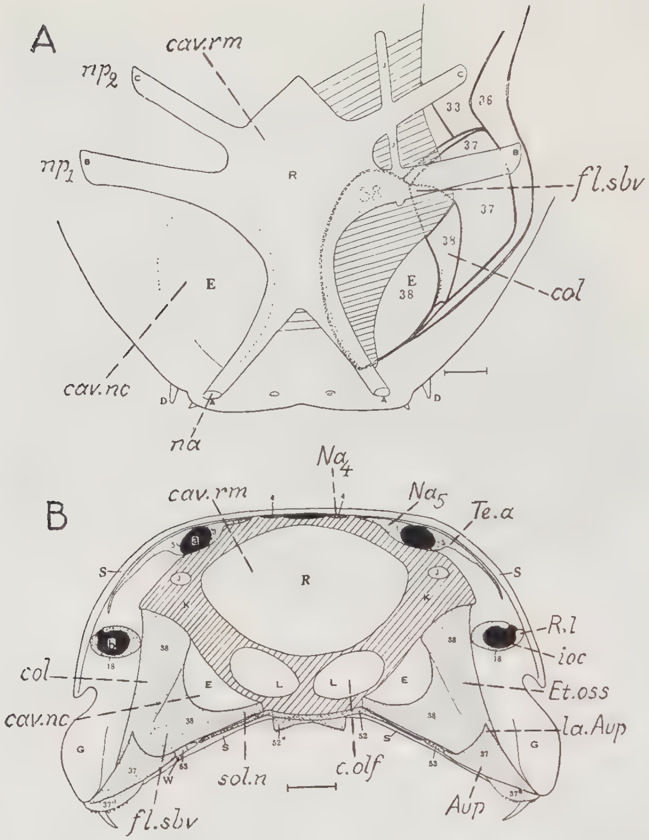

Fig. 83. *Latimeria chalumnae* Smith. *A*, diagram of the snout in dorsal view showing the position of the median rostral cavity and of the nasal cavities and the course of the anterior and posterior nasal tubes according to SMITH. From SMITH (1939, fig. 6). Cartilage removed above the level of the external nostrils. Cartilage denoted with parallel lines, bones with cross-hatched double lines. *B*, transverse section through the snout 40 mm behind the tip. From SMITH (1939, fig. 7). Sensory canals black. Cartilage denoted with parallel lines, cartilage-bones and dermal bones dotted.

Aup, autopalatine; Na_4, Na_5, nasals 4 and 5; *Et. oss*, ethmoidal ossification; *R. l*, lateral rostral; *Te. a.* anterior tectal; *cav. nc*, nasal cavity; *cav. rm*, median rostral cavity; *col*, lateral columnar portion of ethmoidal ossification forming the high posterior division of the lateral nasal wall; *c. olf*, canalis olfactorius; *fl. sbv*, posterior transverse portion of ethmoidal ossification ("subvertical flange"); *ioc*, infraorbital sensory canal; *la. Aup*, ascending lamina of autopalatine; np_1, np_2, posterior external nostrils; *sol. n*, solum nasi (the "fan-shaped base" of the ethmoidal ossification).

Explanation of the lettering of SMITH in his own terms (my own terminology in brackets): *A*, rostral narial aperture and tube (anterior external nostril and anterior nasal tube); *B*, *C*, lower and upper lateral narial aperture and tube (posterior external nostrils and posterior nasal tubes); *D*, rostral papilla; *E*, olfactory capsule (the cavity of the nasal capsule); *G*, pseudo-maxillarial fold; *J*, tube for ophthalmic branches of the V and VII nerves (anterior canal for r. ophthalmicus lateralis); *K*, cartilage; *L*, olfactory lobes of the brain (canalis olfactorius); *R*, ethmoidal nasal cavity (median rostral cavity); *S*, skin; *W*, palatine canal; *a*, parafrontal canal (supraorbital sensory canal); *b*, infraorbital sensory canal; *3*, fronto-nasal (nasal 5); *4*, postrostral (nasal 4); *5*, naso-antorbital (anterior tectal); *18*, latero-rostro-nasal (lateral rostral); *33*, pterygoid (entopterygoid);

condition. In the Devonian Coelacanthids the two posterior external nostrils probably lay close outside the lower part of the posterior tectal, immediately outside the openings (*fe_1exp*, *fe_2exp*, fig. 77 A, B) for the two branches of the posterior external nasal tube (*ntp*, fig. 79). In *Latimeria* the two nostrils have the same position both in relation to one another and to the orbital opening as they must have had in the Devonian forms, but both lie in the skin ventro-laterally to the posterior tectal (*Te.p*, fig. 35), which is certainly due to a reduction of the ventrolateral part of that bone. In this connection it is of interest that the posterior tectal is somewhat reduced ventro-laterally even in certain Coelacanthids from the Lower Triassic (the unnamed form from East Greenland and *Whiteia*; NIELSEN 1936, figs. 8—12; cf. p. 585).

As we have seen above (pp. 565, 571—572), the anterior and posterior external nasal tubes in fossil Coelacanthids must have issued from the nasal sac and thus from the nasal cavity (*nta*, *ntp*, figs. 78 B, 79). In *Latimeria*, on the other hand, the corresponding nasal tubes are said by SMITH (1939, pp. 54—56; see *A*, *B*, *C*, figs. 82, 83 A in the present work) to come from the median rostral cavity, which is completely separated from the nasal cavities. If this were true, the anterior and posterior nasal tubes would thus in *Latimeria* have nothing at all to do with the nasal sac and the nasal cavity. The cavity of the nasal sac would be a completely closed space, and the fenestra endonarina communis would have lost its primary function as an opening for the external nasal tubes. This is, of course, extremely unlikely. Since the nasal cavity, the fenestra endonarina communis and the lateral rostral are developed in *Latimeria* almost exactly as in the fossil Coelacanthids, it must be strongly suspected that SMITH is mistaken as regards the course of the external nasal tubes in *Latimeria*. It would therefore appear highly probable that these tubes in *Latimeria* actually leave the nasal sac through the fenestra endonarina communis in the same way as they did in fossil Coelacanthids (see foot-note 1 on p. 588; cf. also WOODWARD 1940).

The nervous system of the snout is still imperfectly known in *Latimeria*. The r. ophthalmicus lateralis traverses both a posterior and an anterior ophthalmicus lateralis canal (*J*, fig. 83 B; SMITH 1939, pp. 55, 89—91), which are developed fundamentally as in the Devonian Coelacanthids (p. 575; footnote 1 on p. 562). Anteriorly this nerve curves downwards in such a way that it may possibly have entered the nasal

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36, ectopterygoid: *37*, autopalatine; *37″*, autopalatine dental plate (dermopalatine); *38*, ectethmoid (ethmoidal ossification); *52*, parasphenoid; *52″*, dental plate of parasphenoid; *53*, prevomer (prearticular autopalatine part of the palatoquadrate).

cavity (Smith 1939, p. 55). The r. palatinus VII passes forwards in the snout ventrally to the ethmoidal ossification (Smith 1939, p. 103).

The autopalatine ossification (*Aup*, *la. Aup*, *37*, figs. 82, 83; Smith 1939, pp. 77—78; fig. 11; pls. 22, 27) consists of a triangular basal part from which ascends a high lamina (*la. Aup*), three-sided in outline when looked at from the lateral or medial side (as regards the prearticular autopalatine part see foot-note 2 on pp. 608—609). The basal part of the bone extends forward underneath the postero-lateral part of the ethmoidal ossification (cf. p. 586), and extends medially as far as to the broadest part of the parasphenoid (Smith 1939, fig. 12; pl. 27; cf. fig. 77 C above). The anterior margin of the ascending lamina lies just behind the lateral columnar portion of the ethmoidal ossification (fig. 82).

Everything seems to show that the autopalatine ossification in Devonian Coelacanthids was developed fundamentally as in *Latimeria*. The position of the autopalatine ossification in Devonian Coelacanthids in relation to the ethmoidal region was therefore probably somewhat as follows (fig. 77 B, C). Its basal part lay immediately ventrally to the ventro-lateral fossa and formed an almost complete floor of that fossa. The postero-medial corner of the basal part rested against the articular area *art. Aup* (fig. 74), and the ventro-medial border of the same part was in contact with the facet $art_a Aup$ along the ventro-medial margin of the ventro-lateral fossa. The ascending lamina (*la. Aup*, fig. 77 B) extended upwards into and filled up the larger part of the fossa ventrolateralis. The dorsal angle of this lamina lay close below the rough area of the ventro-lateral fossa, to which (and to the process *pr. lig*, figs. 74 B, 76 B) the angle was probably attached by ligaments.

e. General remarks.

As shown above, the snout in Coelacanthids has undergone but few changes since the Middle Devonian. The snout in *Latimeria* is essentially as in the Mesozoic Coelacanthids and thus differs only in certain characters of minor importance from the snout of the Devonian forms, chiefly owing to a regressive development of the endoskeletal bone tissue, the endoskeleton, and the dermal bones. In the Middle Devonian *Dictyonosteus* the whole anterior division of the endocranium is occupied by a large ethmosphenoid bone similar to that of Rhipidistid Crossopterygians. The anterior parts of that bone in *Dictyonosteus* lie in the snout and consist not only of perichondral but also to a large extent of enchondral bone. In the Upper Devonian forms the endocranial parts of the snout are still occupied by the ethmosphenoid, which in these forms, however, is chiefly made up of perichondral bone layers. The enchondral bone tissue has disappeared to a large extent and the interior of the ethmosphenoid consisted almost entirely of cartilage. In the Postdevonian forms, all that is known to persist of the ethmosphenoid in the snout is a comparatively small paired bone, the ethmoidal ossification, situated in the posterior ventro-lateral part of the etmoidal region. In *Latimeria* there is also, as in Postdevonian fossil forms, only a paired ethmoidal ossification. It thus appears that the regressive development of the bone tissue in the endocranial parts of the snout proceeded rapidly during the Devonian but ceased in the lower Carboniferous without resulting in a complete secondary chondrification of the endoskeleton. Apparently the posterior ventro-lateral part of the postnasal wall with the fossa ventro-lateralis has become entirely reduced in *Latimeria.* The dermal bones of the outside of the snout in *Latimeria* are undoubtedly more reduced than in the Devonian and most of the Postdevonian fossil forms. Reductions in the external dermal bones are, however, met with also in certain Triassic forms (*Axelia,* Stensiö 1932, fig. 15 B; *Whiteia,* and another, unnamed form, Nielsen 1936). Finally it deserves to be mentioned that the sensory canal system of the snout has become modified in Coelacanthids by the widening of the canals and by the development of secondary commissures (fig. 32; pp. 335—339), so that it is considerably more complicated in Mesozoic forms and recent *Latimeria* than in Devonian forms.

2. Comparative section.

a. Comparison with Porolepiformes and Osteolepiformes (Rhipidistia).

It is fully evident from the present investigations that in most respects the snout of Coelacanthids is very different from that of *Porolepiformes* and *Osteolepiformes.* The most important characters in which the snout of Coelacanthids differs from that of Rhipidistid Crossopterygians may be briefly summarized as follows.

1) The absence of a choana. There is no fenestra endochoanalis leading down to the mouth cavity and the nasal cavity has no direct connection with the mouth cavity. Conformably there is neither a lateral recess in the nasal cavity nor equivalents of the structures that in *Porolepiformes* and *Osteolepiformes* lay behind that recess.

2) The presence of a large fenestra endonarina communis. In *Osteolepiformes* and at least in *Porolepis* the fenestra endonarina anterior and the fenestra endonarina posterior are separate openings.

3) The development of the posterior external nasal tube, which is divided into two branches leading outwards to two separate posterior external nostrils on either side.

4) The presence in the nasal cavity of an antero-medial and a postero-dorso-lateral recess lacking equivalents in *Porolepiformes* and *Osteolepiformes.*

5) The absence of an equivalent of the crista rostro-caudalis in *Porolepiformes* and the absence of equivalents of all the crests and ridges through which the nasal cavity in *Osteolepiformes* is subdivided into a recessus superior, a recessus medius, a recessus inferior, and recesses for the nasal muscles.

6) The development of the internasal wall, which is thick in its upper and posterior parts and encloses a median rostral cavity not present either in *Porolepiformes* or *Osteolepiformes.*

7) The absence of equivalents of the cavum internasale of the *Porolepiformes* and of the prenasal pit of the *Osteolepiformes.*

8) The powerful development and considerable rostro-caudal extent of the postnasal wall.

9) The presence of the paired fossa ventro-lateralis in the antero-lateral part of the postnasal wall (except in *Latimeria*).

10) The absence of an olfactory ridge both on the interorbital wall and on the posterior face of the postnasal wall. The absence also of a crista suspendens.

11) The development and position of the pars autopalatina of the palatoquadrate and the development of the articular connection of the pars autopalatina with the ethmoidal region.

12) The development of the canalis olfactorius with a long, high and narrow division for the bulbus olfactorius and a comparatively short one for the n. olfactorius. In *Porolepiformes* and *Osteolepiformes* the bulbus olfactorius was short and the n. olfactorius long. In *Porolepiformes* the bulbus olfactorius also had quite a different position in relation to the hemisphere than it had in Coelacanthids.

13) The apparent absence of any lateral nasal branch of the n. profundus. In *Porolepiformes* and *Osteolepiformes* this nerve divided into one medial and one or several lateral nasal branches.

14) The course of the r. buccalis lateralis and r. maxillaris V in relation to the nasal cavity. These two nerves entered the nasal cavity at the postero-ventral corner of the fenestra endonarina communis and then traversed the ventro-lateral part of the nasal cavity. If one of the branches of the r. buccalis lateralis in *Porolepiformes* possibly entered the nasal cavity, it must have reached that cavity from behind through the postnasal wall and not from the lateral side as in Coelacanthids.

15) The presence of a canal for the orbitonasal artery. No corresponding canal exists either in *Porolepiformes* or *Osteolepiformes.*

16) The development of the vascular system of the snout as a whole.

17) The position of the places of origin of the mm. obliqui of the eye and the presence of small anterior myodomes.

18) The absence of an intermaxillary gland and of all structures developed in relation to such a gland.

19) The absence of a palatal lamina of the ethmoidal shield.

20) The development of the lateral rostral. This bone has an anterodorsal process but is devoid of any process comparable either to the processus dermintermedius of *Osteolepiformes* or to the palatal process of *Porolepiformes* and *Osteolepiformes*. In addition it is of a different shape.

21) The shape and forward extent of the parasphenoid. This bone is broad anteriorly as in *Porolepiformes* but extends forwards underneath the ethmoidal region almost to the transition between the internasal wall and the divisio prenasalis communis as it does in *Osteolepiformes*.

22) The development and position of the vomers. These bones, which become much reduced in Coelacanthids of later geological periods, are weakly developed and devoid of vertical tooth-bearing laminae and posterior processes. They generally lie far forward and fairly close to each other.

23) The course of the infraorbital sensory canal far dorsally along the lateral side of the thick postnasal wall (cf. pp. 335, 602) and the presence of anterior and posterior transverse commissures between the infraorbital and supraorbital canals. These commissures are perhaps old formations homologous to those in Brachiopterygians and Actinopterygians (cf. pp. 602, 618 and foot-note 1 on pp. 605—606).

24) The manner in which the reduction of the bone tissue of the endocranial parts of the snout took place and the results of that reduction. In Coelacanthids the reduction commenced in the internasal wall and proceeded backwards in such a way that in the Postdevonian forms there persists only a paired ethmoidal ossification in the postero-ventrolateral part of the ethmoidal region. In Urodeles and Anurans, which we have seen (pp. 422, 451) must be regarded as descendents from *Porolepiformes* and *Osteolepiformes* respectively, the reduction took place in a somewhat different manner. It began in the superficial anterior and lateral parts of the ethmoidal region in *Porolepiformes* and *Osteolepiformes* and then proceeded in such a way that in Urodeles and Anurans there persists an unpaired median bone, the orbitosphenoid or sphenethmoid, in the hinder part of the ethmoidal region and the anterior parts of the interorbital wall. In Urodeles there also sometimes persists a small ossification, the nariodal bone (pp. 293—295, 402), in the lateral nasal wall.

Apart from the disposition of the sensory canal system and certain general features in the pattern of the dermal bones, the snout in Coelacanthids is of a type fundamentally different from that of *Porolepiformes* and *Osteolepiformes*. The Coelacanthids as a group are thus very distinct from the *Porolepiformes* and *Osteolepiformes*, which certainly are greatly different but nevertheless are much more closely related to each other than to the Coelacanthids. It is therefore necessary to classify the Coelacanthids in a large group of their own among the Crossopterygians (see p. 241).

As the differences enumerated above between Coelacanthids and Rhipidistids are partly of a fundamental nature it might possibly even be suggested that the Coelacanthids be removed from the Crossopterygians and placed in a group of the same systematic rank as *Dipnoi*, *Crossopterygii*, *Brachiopterygii* and *Actinopterygii*. At least for the present, however, I cannot see that we are justified in doing so, for apart from the development of the snout and certain other conditions it cannot possibly be denied that they show several fundamental points of agreement with the Rhipidistids, e. g. the following (see HOLMGREN and STENSIÖ 1936, pp. 344—363; SÄVE-SÖDERBERGH 1936, pp. 136—147; ROMER 1937; cf. pp. 493—494): 1) The cranium is subdivided into two large divisions, the divisio cranialis anterior and the divisio cranialis posterior; 2) The ossifications in the endocranium of Devonian Coelacanthids consist of two large unpaired bones, the ethmosphenoid and the otico-occipital (cf. WATSON 1925, pp. 846—849; 1926, fig. 1; STENSIÖ 1932, pp. 17—18, fig. 8; HOLMGREN and STENSIÖ 1936, figs. 264—269; SÄVE-SÖDERBERGH 1936, fig. 58; ROMER 1937, figs. 1—7); 3) The posterior part of the ethmosphenoid is provided with two processes, the antotical process and the basal process, which were in articular connection with the palatoquadrate (cf. No. 5 on p. 494); 4) The ethmosphenoid has a posterior process, the processus connectens, for the connection with the otico-occipital (cf. No. 6 on p. 494); 5) The canal for the notochord is wide and extends forwards to a wide pit in the posterior end of the ethmosphenoid (cf. No. 7 a on p. 494). This wide canal causes the posterior parts of the cranial cavity to be situated high above the basis cranii; 6) The majority of the nerve canals and vascular canals behind the snout are developed very similarly to what they are in *Osteolepiformes*; 7) The disposition of the sensory canal system of the head is of the Rhipidistid type; 8) The general pattern of the dermal bones of the head is Rhipidistid-like (see e. g. HOLMGREN and STENSIÖ 1936, pp. 355—363; figs. 273—277; STENSIÖ 1937 a, figs. 1—4; SÄVE-SÖDERBERGH 1941, fig. 3; J. L. B. SMITH 1939, fig. 5; cf. also figs. 33—35 in the present work); 9) The endoskeletal elements supporting the two dorsal fins and the anal fin are concentrated and more or less modified in a Rhipidistid-like manner (STENSIÖ 1932, pp. 65—70; this feature as regards the anterior dorsal and anal fins shared with primitive Dipnoans, e. g.

Fleurantia, Graham-Smith and Westoll 1937). — These characters seem decidedly to indicate that Coelacanthids and Rhipidistids must be classified in a common group, but the differences in the structure of the snout and in other respects prove that they have undergone a long development independently of each other.

b. Comparison with Elasmobranchs.

As regards the snout the Coelacanthids differ from the Elasmobranchs (*Chlamydoselachus*, figs. 2—4; pp. 250—256) inter alia in the following respects. The ventral parts of the internasal wall are devoid of an equivalent to the subethmoidal depression. The median rostral cavity, like the cavum precerebrale of sharks, lies in the dorsal parts of the internasal wall and was presumably occupied by the brain in embryonic stages, but it is separated by a wall of cartilage from the cranial cavity and has a cartilaginous roof. The solum nasi is complete and has no perforation corresponding to the nasal fontanelle. The nasal cavity lies with its ventral parts fairly close to that of the opposite side and has two recesses, antero-medial and postero-dorso-lateral. The nostrils are situated high up on the lateral side of the snout. There are two posterior external nostrils which lie behind the nasal cavity, between that and the orbital opening. The bulbus olfactorius emerged directly from the anterior parts of the brain and there was no tractus olfactorius between it and the hemisphere. The n. profundus, the r. maxillaris V, the r. buccalis lateralis and perhaps also the r. ophthalmicus lateralis all entered the nasal cavity. There is a canal presumably for the a. orbitonasalis, which leads from the orbit to the canalis olfactorius. The canal for the v. cerebralis anterior is short and pierces the antero-dorsal part of the lateral cranial wall. There is a canal probably for a vein leading from the cranial cavity to the middle dorsal part of the orbit. The places of origin of the mm. obliqui of the eye are widely separated and dorsal and ventral anterior myodomes are developed. The supraorbital sensory canal passes forwards medially to the external nostrils and anastomoses with the infraorbital sensory canal close to the rostral tip of the snout. The infraorbital canal passes forwards and downwards on the lateral side of the snout and crosses the lower part of the fenestra endonarina communis. In advanced forms there still persists a paired ossification in the ethmoidal region and in addition also an ossification in the pars autopalatina of the palatoquadrate.

What has now been said may suffice to show that the snout in Coelacanthids is of a type quite different from that in Elasmobranchs. (As regards the dermal bones cf. p. 389).

c. Comparison with Brachiopterygii (Polypterus).

As described above (pp. 262—265, fig. 9) the arrangement of the nerves and vessels in the snout of *Polypterus* is of a distinct type. At least the Devonian Coelacanthids (fig. 78 B; pp. 578—579) seem to have had an a. ophthalmica and a v. ophthalmica developed very much as those in *Polypterus*. Thus the v. ophthalmica seems to have arisen by the confluence of a medial ($v.\ o_m$) and a lateral ($v.\ o_l$) branch and also received two tributaries from the cranial cavity, one of which left the cranial cavity together with or close to the n. trochlearis. Both the a. ophthalmica and the v. ophthalmica of the Devonian forms accompanied the r. ophthalmicus lateralis in the anterior ophthalmicus lateralis canal (*c. o. lat.* figs. 75, 76, 78 A), which has a position resembling that of the profundus canal in *Polypterus* (*c. pr*, figs. 5 A, 6; p. 260) and like that may be widened in its hindmost part to form a dorsal anterior myodome. The n. profundus in the Devonian Coelacanthids also resembled the corresponding nerve in *Polypterus*[1] in its ramification and by entering the nasal cavity. On the other hand it differed from the nerve in *Polypterus* by piercing the postnasal wall lower down in a canal of its own (cf. No. 1 on p. 611) and reaching the nasal cavity from behind and not from above.

Both in *Polypterus* (pp. 260, 263; figs. 5 A, 7, 9) and Coelacanthids (p. 576; figs. 73 B, 75, 76 B, 78 A, 79) a canal (*c. a. on*) is developed which from the anterior ventral part of the orbit leads to the canalis olfactorius. This canal is remarkable, for as far as I can see it is difficult to find an equivalent to it in other groups of lower Gnathostomes. In *Polypterus* it is traversed by the a. orbitonasalis and it is thus likely that it was developed for that artery also in Coelacanthids. This canal has therefore also in the latter been referred to as the canal for the orbitonasal artery. As far as we know, in *Polypterus* it ends at its connection with the canalis olfactorius, but in Coelacanthids it also has an anterior part continuing forwards from the connection with the canalis olfactorius and uniting with the profundus canal This foremost part in Coelacanthids may have transmitted a branch of the orbitonasal artery but its presence may probably also mean that the canal for the orbitonasal artery in them housed also some other structure, either a vein draining the ventro-medial parts of the nasal cavity (cf. the orbitonasal vein in *Chlamydoselachus*, p. 256; the nasal vein in *Amia* p. 269 and the vein traversing the "orbitonasal canal" of De Beer's description in *Acipenser*; p. 269; c_2on, fig. 10 A) or perhaps a nerve anastomosis (e. g. corresponding to the anastomosis between the r.

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[1] As in Selachians, Dipnoans, Crossopterygians and Amphibians the n. profundus in *Polypterus* represents the ventral branch of the nerve (cf. p. 268 above).

maxillaris V and the n. profundus in *Protopterus*, p. 283, fig. 15). The orbital orifice of the canal for the orbitonasal artery in Coelacanthids is widened so as to form an anterior ventral myodome (my_v, figs. 75, 76 B, 78 A) and thus obviously served as a place of origin of the m. obliquus inferior. In *Polypterus* the m. obliquus inferior (*m. obl. i*, fig. 9) also arises far below the m. obliquus superior, more precisely somewhat in front of the orbital orifice of the canal for the a. orbitonasalis, and its place of origin does not differ very much from that in Coelacanthids.

At least in fossil Coelacanthids (fig. 78 B) the r. buccalis lateralis, presumably accompanied by the r. maxillaris V (*r. mx + buc*), the a. maxillaris (*a. mx*) and the v. infraorbitalis (*v. io*), went forwards to the nasal cavity through the fossa ventro-lateralis, laterally to the ascending lamina (*la. Aup*, fig. 77 B) of the autopalatine ossification and to the presumed ligament connecting that lamina with the ethmoidal region. It entered the nasal cavity either as in *Nesides* and *Euporosteus* at the very postero-ventral corner of the fenestra endonarina communis in a canal (*c. buc*, fig. 77) between the lateral nasal wall and the lateral rostral, or, as in *Diplocercides*, *Axelia*, and *Undina* (*lat. for*, pp. 561, 583), through a short canal in the lateral nasal wall close behind the fenestra endonarina communis. In *Polypterus* the r. buccalis lateralis, the r. maxillaris V, the a. maxillaris and the v. infraorbitalis (*r. mx + buc*, *a. mx*, *v. io*, fig. 9) pass forwards close laterally to a ligament attaching the autopalatine ossification to the endocranium and thus morphologically laterally to the autopalatine ossification (see p. 263 above). They then continue forwards and enter the nasal cavity either, in larvae, through the postero-ventral corner of the fenestra endonarina communis (*fe. en + buc*, fig. 6 A) or, in adults, through a foramen in the lateral nasal wall (*f. buc*, figs. 6 B, 7, 9; cf. pp. 259—260) situated behind the postero-ventral corner of the fenestra endonarina communis. As regards the passage of these nerves and vessels from the orbit to the nasal cavity we thus find a very striking agreement between Coelacanthids and *Polypterus*.

The r. palatinus VII in *Latimeria* is said by Smith (1939, p. 103) to pass ventrally to the ethmoidal ossification and the foremost non-dentigerous part of the parasphenoid but dorsally to the "dental plate of the prevomer" (see *W*, fig. 83 B; Smith 1939, fig. 12). In *Polypterus* the medial (anterior) branch of the r. palatinus ($r. pal_m$, fig. 9; p. 263) goes forwards medially to the "mesial dermopalatine" (Allis 1922, p. 281; cf. Goodrich 1930, fig. 296 B, *vo*) and thus ventrally to the non-dentigerous portion of the foremost part of the parasphenoid (cf. fig. 5 B), and then continues forwards dorsally to the "mesial dermopalatine". Since the last-mentioned bone beyond doubt corresponds to the "dental plate of the prevomer" in *Latimeria* (predermopolatine, p. 608), it is obvious that the medial branch of the r. palatinus VII in *Polypterus* has a course corresponding exactly to that of the r. palatinus VII in *Latimeria*.

The anterior part of the cranial cavity in Coelacanthids (*cav. cr*, figs. 75, 78 A; p. 572; SMITH 1939, figs, 15, 16; p. 91) is of such a shape that it may very well be imagined to have housed a forebrain resembling that in *Polypterus* (fig. 8; cf. WALDSCHMIDT 1887, figs. 3—5; BING and BURCKHARDT 1905, figs. 29—31). The bulbi olfactorii both in Coelacanthids (figs. 78 B, 79; pp. 572—573) and in *Polypterus* (figs. 7, 8; p. 262) lie in the hinder parts of the canales olfactorii and are completely separated from each other. They are high and narrow but comparatively long, whereas the nn. olfactorii (*I*), lodged in the foremost parts of the olfactory canals, are short and thick. It may be added that a pineal foramen is lacking in both Coelacanthids and *Polypterus* and that the parasphenoid is pierced by a hypophysial canal (LEHN 1918, fig. 11; DE BEER 1926; ALLIS 1931; GÉRARD and CORDIER 1937; STENSIÖ 1937 a, p. 10; figs. 5 C—E, 8 A; pl. 12, fig. 2; WESTOLL 1939, pp. 10, 16—17, figs. 1 b, 4 b).

Judging from the shape of the nasal cavity, the nasal sac in *Nesides* and *Euporosteus* (*sac n*, figs. 78 B, 79) was short and high, about as in larvae of *Polypterus* (MARCUS 1930, figs. 26, 27), whereas in *Diplocercides* (cf. pl. 16, fig. 3) it was longer, narrower and possibly of an egg-shaped type somewhat similar to that in the adult *Polypterus* (figs. 7, 8). It is of particular interest that the nasal cavity in Coelacanthids has an antero-medial recess (*re. am*, fig. 76 A) situated as the antero-medial recess of the nasal cavity in *Polypterus* (fig. 7) and undoubtedly like that housing an antero-medial diverticle (*di. am*, figs. 7, 79) of the nasal sac. Approximately opposite the antero-medial diverticle in Coelacanthids both the anterior external nasal tube and the posterior external nasal tube (*nta*, *ntp*, figs. 78 B, 79) passed off from the antero-lateral part of the nasal sac quite as in *Polypterus* (fig. 7). Neither Coelacanthids nor *Polypterus* have a choana. The posterior external nasal tube of Coelacanthids differs somewhat from that in *Polypterus*, as it divided into two branches which opened outwards through separate openings. Consequently there were two posterior external nostrils in Coelacanthids whereas there is only one in *Polypterus*.

From the above it will readily be seen that in the general development of the forebrain and olfactory nerves, the shape of the nasal sac, and the course of the nerves and vessels of the snout the Coelacanthids are or must have been strikingly similar to *Polypterus*. As we shall now see, they also present several points of agreement with *Polypterus* in the development of the skeleton.

The nasal cavity is very similar in Coelacanthids and *Polypterus*. In both it is provided with very complete walls and opens outwards through a large fenestra endonarina communis (*fe. en*) in the anterior part of the lateral nasal wall.

In *Polypterus* the internasal wall is a thin nasal septum (*sn*, fig. 7). In the Coelacanthids it is fairly thin and solid only most ventrally, whereas dorsally it attains a considerable breadth and (at least in *Latimeria*) houses the median rostral cavity (*cav. rm*, figs. 79, 82, 83; p. 587). The development of the internasal wall is thus fairly different in *Polypterus* and Coelacanthids. In larvae of *Polypterus*, however, the brain extends far forwards and its foremost part lies dorso-medially to the posterior parts of the nasal sac in the dorsal parts of the internasal wall and in a space which reminds strikingly of the median rostral cavity in *Latimeria*. Like that cavity this space has only a thin roof of cartilage close underneath the dermal bones of the dorsal side of the snout and is separated ventro-laterally by a thin wall (in *Polypterus* partly made up of connective tissue) from the nasal cavity of either side (compare the transvere section through the median rostral cavity and the posterior parts of the nasal cavities in *Latimeria*, fig. 83 B, with the transverse sections through the corresponding parts of the snout in larvae of *Polypterus* reproduced by LEHN 1918, fig. 16, and by MARCUS 1930, fig. 28 m). The position and shape of the nasal cavity in larvae of *Polypterus* as seen in transverse sections also remind considerably of conditions in *Latimeria*. These points of agreement between Coelacanthids and *Polypterus* support the opinion advanced above (p. 587) that the median rostral cavity in Coelacanthids is simply a persisting part of the embryonic ethmoidal part of the cranial cavity.

The divisio prenasalis communis is well developed both in Coelacanthids (fig. 79) and *Polypterus* (fig. 7). In Coelacanthids (figs. 73, 74 A) it is produced anteriorly, as in larvae of *Polypterus* (fig. 6 B), into a dorsal and a ventral rostral process (*pr. rd*, *pr. rv*) separated by a transverse groove ($gr_c ioc$) for the ethmoidal commissure of the infraorbital sensory canals. In the adult *Polypterus* the ventral rostral process is strongly produced forwards (*pr. rv*, fig. 7) and thus much more pronounced than the dorsal one.

The postnasal wall (*w. pn*) of *Polypterus* (figs. 5—7, 9), as that of *Latimeria* (cf. p. 587), differs from that of Devonian Coelacanthids (figs. 73—76, 79) above all by the absence of an equivalent to the postero-lateral part with the fossa ventro-lateralis (*fo. vl*).

Along the ventro-medial margin of the fossa ventro-lateralis, on the lower face of the postnasal wall, Devonian Coelacanthids have a marked facet ($art_a Aup$, fig. 74) for the medial border of the autopalatine, extending forwards and laterally from a point close to the lateral border of the broad anterior part of the parasphenoid. This facet agrees most strikingly in position and extent with the articular facet for the pars autopalatina of the palatoquadrate on the lower face of the ethmoidal region in *Polypterus* (*art. aup*, figs. 5, 6 B).

Both in Coelacanthids and in *Polypterus* we find an independent autopalatine ossification (*Aup*, *37*, figs. 5 A, 9, 77 B, C, 80, 82, 83) and a paired ethmoidal ossification (*Et. oss*, figs. 5, 7, 9, 80—83). Coelacanthids and *Polypterus* differ in this respect considerably from the Rhipidistid Crossopterygians, where the bones just referred to are not developed as independent elements, and approach Actinopterygians (cf. No. 24 on p. 595 and Nos. 1, 2 on p. 613).

We shall now proceed to a comparison of the sensory canals and dermal bones of the snout in Coelacanthids and *Polypterus* (Traquair 1870; Pollard 1892; Allis 1900 a; 1919 a; 1922; Goodrich 1909, fig. 266; 1930, fig. 296; Holmgren and Stensiö 1936, pp. 393—398).

Both in Coelacanthids (fig. 32; p. 334) and *Polypterus* (figs. 5 A, 84; Allis 1900; Pehrson 1922, fig. 24) the supraorbital sensory canal (*soc*) goes forwards medially to the external nostrils and anastomoses with the infraorbital canal antero-medially to the anterior external nostril and close to the rostral tip of the snout. Immediately behind its anastomosis with the infraorbital canal in *Polypterus* it gives off a postero-ventro-lateral branch situated immediately behind the proximal part of the anterior external nasal tube. The position and course of this branch, which is currently regarded as the foremost end of the supraorbital sensory canal, reminds considerably of the anterior transverse commissure in Coelacanthids (*com. tra*, figs. 32 B, C, 35, 80; cf. foot-note 1 on p. 605).

The infraorbital sensory canal (*ioc*) also has a very similar course in the snout in Coelacanthids (figs. 32, 35, 77; p. 335) and *Polypterus* (figs. 5 A, 84; see also e. g. Pehrson 1922, fig. 24; Holmgren 1942, fig. 23). Thus it first bends upwards in front of the orbital opening so that for some distance it passes far dorsally along the lateral side of the postnasal wall. Then it runs forwards and downwards across the ventral part of the fenestra endonarina communis, and in front of that it curves medially and joins its fellow of the opposite side to form the ethmoidal commissure.

In Coelacanthids (figs. 35, 77) the preorbital part of the infraorbital sensory canal pierces the anterior part of the complex lachrymo-jugal (*La-Ju*), the lateral rostral (*R. l*) and a transverse row of medial rostrals (*R. m*), which at least in *Mylacanthus* or *Scleracanthus*? (Stensiö 1921, fig. 51) and *Latimeria* (fig. 35) are three in number on either side of the median line. These bones are as a rule developed as tubes around

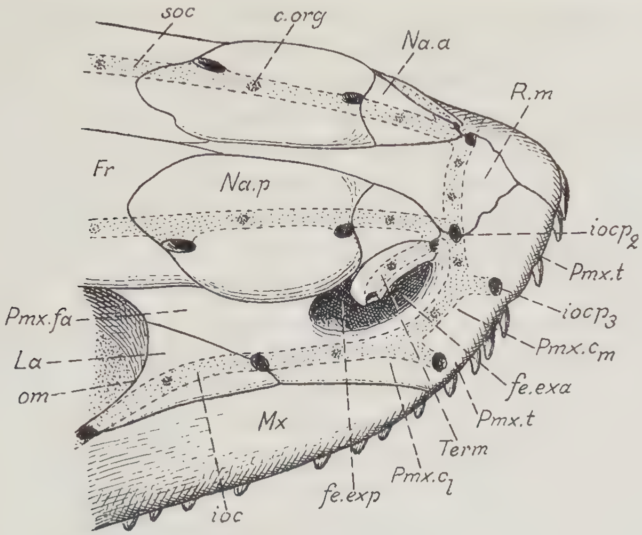

Fig. 84. *Polypterus senegalus.* Dermal bones and sensory canals of the snout in dorso-lateral view. Same specimen as in fig. 5. The position of the sensory canal organs after ALLIS (1900). $^4/_1$.

Fr, frontal; *La,* lachrymal; *Mx,* "maxillary" (tooth-bearing portion); *Na. a, Na. p,* anterior and posterior nasals; *Pmx.* c_l, *Pmx.* c_m, postero-lateral longitudinal and antero-medial transverse sensory canal portions of "premaxillary" (tecto-rostro-premaxillary); *Pmx. fa,* postero-dorsal facial portion of "premaxillary"; *Pmx. t,* tooth-bearing portion of "premaxillary"; *R. m,* median rostral; *Term,* terminal; *c. org,* sensory canal organs; *fe. exa,* fenestra exonarina anterior; *fe. exp,* fenestra exonarina posterior; *ioc,* infraorbital sensory canal; *iocp*$_2$, *iocp*$_3$, second and third pore of ditto; *om,* margin of orbital opening; *soc,* supraorbital sensory canal.

the infraorbital canal, which normally is fairly wide. In *Polypterus* the preorbital part of the infraorbital canal (*ioc*, figs. 5 A, 84; TRAQUAIR 1870; ALLIS 1900; 1900 a; 1922; GOODRICH 1930, fig. 296; HOLMGREN and STENSIÖ 1936, figs. 297, 298) traverses the small lachrymal (*La*), the sensory-canal-bearing "premaxillary" and the median rostral (*R. m*; "ethmoid", TRAQUAIR; ALLIS).

The median rostral in *Polypterus* lodges the foremost sensory canal organ of the infraorbital canal of either side, thus altogether two organs, and must be a complex bone formed by the fusion of two medial rostral elements (the medialmost medial rostral of either side; cf. STENSIÖ 1921, p. 275; PEHRSON 1922, p. 43; HOLMGREN and STENSIÖ 1936, p. 393). The position of this medialmost rostral element of either side was obviously very much as that of the medialmost one of the three paired medial rostrals in *Latimeria* (bone No. *20*, fig. 35). The median rostral in *Polypterus* has a narrow posterior part, which extends far backwards on the upper side of the ethmoidal region. This narrow posterior part is probably comparable to the postrostrals in Coelacanthids (*Ptr*, fig. 35; cf. p. 352; cf. also Stensiö 1921, p. 275).

The so-called premaxillary in *Polypterus* (figs. 5, 9, 84) may be considered to have four portions (for particulars see Allis 1900 a, pp. 257—262): 1) a tooth-bearing portion (*Pmx. t*) with a palatal lamina (*Pmx. pal*), 2) an antero-medial transverse sensory canal portion (*Pmx.* c_m), 3) a postero-lateral longitudinal sensory canal portion (*Pmx.* c_l), and 4) a postero-dorsal facial portion (*Pmx. fa*).

Leaving out of the question the palatal lamina, which is without equivalent in Coelacanthids, the tooth-bearing portion of the "premaxillary" in *Polypterus* (*Pmx. t*) agrees well both in position and extent with the premaxillary of Coelacanthids (*Pmx*, fig. 81; cf. Goodrich 1909, fig. 261 A, B; Watson 1921, figs. 4, 5; Nielsen 1936, fig. 14). The antero-medial transverse sensory canal portion of the "premaxillary" in *Polypterus* (*Pmx.* c_m) lies dorsally to the lateral larger part of the tooth-bearing portion and is developed in such a way that in posterior view it "looks decidedly like a separate cylindrical bone" (Allis 1900 a, p. 261). On account of this and as it lodges two sensory canal organs (the second and third sensory canal organs of the infraorbital sensory canal counted from the front), it is readily seen that this sensory canal portion is comparable to the two lateral ones of the three medial rostrals of either side in *Latimeria* (bones Nos. *21*, *22*, fig. 35).

The homology of one half of the sensory canal portion of the median rostral (*R. m*, fig. 84) and the antero-medial transverse sensory canal portion (*Pmx.* c_m) of the "premaxillary" in *Polypterus* with the three medial rostrals (bones Nos. *20*, *21*, *22*, fig. 35) in Coelacanthids is borne out also by the following facts. 1) In *Polypterus* the supraorbital sensory canal anastomoses with the infraorbital sensory canal just at the suture between the median rostral and the antero-medial transverse sensory canal portion of the "premaxillary", that is to say between the medialmost and middle ones of the three primary rostral components. Supposing that the sensory canal denoted *soc*? (fig. 32 C; p. 339) is the primary anastomosis of the supraorbital with the infraorbital canal, which seems very likely, the corresponding anastomosis in *Latimeria* also lies between the medialmost and the middle ones (bones Nos. *20* and *21*, fig. 35) of the three rostrals, as it does in *Polypterus*. 2) In *Latimeria* the anterior external nostril (*na*, *A*, fig. 35) is situated between the middle and the lateral medial rostrals (bones Nos. *21* and *22*). As pointed out above (p. 589), however, this position of the anterior external nostril in *Latimeria* is certainly secondary. Conditions in fossil Coelacanthids show that the anterior external nostril in that group must primarily have been situated somewhat further backwards, just behind the suture between the middle and lateral medial rostrals, between these two bones and the antero-dorsal process (*pr. R. l*, figs. 77 B, 80) of the lateral rostral. In *Polypterus* the anterior external nasal tube (*nta*, fig. 7) is secondarily produced, but its proximal part lies close postero-dorsally to the sensory canal tube *iocp*$_3$ (fig. 84), which is situated approximately at the place where the suture between the primary independent middle and lateral medial rostrals may be suspected to have passed. The position of the proximal part of the anterior external nasal tube in relation to the medial rostrals is thus quite the same in Coelacanthids and *Polypterus*.

The postero-lateral longitudinal sensory canal portion of the "premaxillary" in *Polypterus* (*Pmx. c*$_l$, figs. 5 B, 84) consists of a tube-shaped piece of bone connecting the anterior tooth-bearing and the antero-medial transverse sensory canal portions with the postero-dorsal facial portion. Both anteriorly and posteriorly it "presents strongly the appearance of overlapping externally, and being fused with," the anterior and postero-dorsal portions of the bone (ALLIS 1900 a, p. 261). It has an oblique position and rises backwards. Another characteristic feature is that it covers the ventral part of the fenestra endonarina communis from the outside. In view of its position, development and other relations it is clear that this portion corresponds to the tube-shaped sensory-canal-bearing part of the lateral rostral in Coelacanthids (fig. 77).

The lateral rostral in Coelacanthids is, as we have seen, provided with an antero-dorsal process (*pr. R. l*, figs. 35, 77 B, 80) situated just outside the fenestra endonarina communis and dividing the dorsal part of that fenestra into two divisions, an anterior one for the anterior external nasal tube, and a posterior one through which the posterior external nasal tube left the nasal cavity. At least in Mesozoic Coelacanthids and in *Latimeria* the antero-dorsal process is pierced by a lateral part of the anterior transverse sensory canal commissure (*com. tra*, figs. 32 B, C, 35, 80), which, as demonstrated by the conditions in the unnamed Triassic Coelacanthid preliminarily described by NIELSEN (fig. 32 B; p. 338), apparently is developed from the supraorbital sensory canal. The antero-dorsal process thus reminds very much of the so-called terminal in *Polypterus* (*Term*, fig. 84), agreeing with that bone in its position in relation to the endocranium, the nasal tubes and the supraorbital sensory canal.[1] On account of this and in view of the similarities otherwise in the structure of the snout in Coelacanthids and *Polypterus* the conclusion readily suggests itself that the antero-dorsal process and the terminal are probably homologous formations. Since they are situated ventro-laterally to the nasal series and dorso-medially to the longitudinal part of the rostral series they must then be regarded as tectals. The bone in Coelacanthids termed lateral rostral in this paper must thus probably be a complex rostro-tectal.

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[1] In the undetermined Triassic Coelacanthid preliminarily described by NIELSEN (1936) the anterior transverse commissure, incomplete in this form, is situated in a groove on the external side of the antero-dorsal process of the lateral rostral (pp. 584—585). As the single lateral rostral of a Devonian Coelacanthid so far known showing the dorso-lateral process is exposed from the inner side (pl. 16, fig. 2), it is quite possible that the anterior

The postero-dorsal facial portion of the "premaxillary" in *Polypterus* (*Pmx. fa*, figs. 5, 84) covers an area of the dorsal face of the ethmoidal region between the upper part of the fenestra endonarina communis and the orbit. However, it also extends somewhat further backwards beyond the ethmoidal region and takes part in the anterior boundary of the orbital opening. According to Holmgren and Stensiö (1936, p. 393) it presumably arises from a separate primordium. The postero-dorsal facial portion of the "premaxillary" in *Polypterus* is thus in all respects as the posterior tectal (*Te. p*, fig. 77 A, B) in Coelacanthids, and may be assumed to correspond to that bone. The fact that the posterior external nasal tube lies entirely outside the facial portion of the "premaxillary" whereas in fossil Coelacanthids it is enclosed in the anterior part of the posterior tectal, has no bearing upon this homologation.

The lachrymal in *Polypterus* (*La*, figs. 5 A, 84) agrees well as regards position and shape with the lachrymal part of the lachrymo-jugal (*La-Ju*, fig. 77 A, B) in Coelacanthids.

The supraorbital sensory canal in *Polypterus* pierces two nasals (*Na. a*, *Na. p*, fig. 84), which agree well with the so-called postrostrals in the Coelacanthid form *Mylacanthus* or *Scleracanthus*? (Stensiö 1921, fig. 51) now to be regarded as nasals (cf. foot-note on p. 352).

The so-called maxillary in *Polypterus* (*Mx-Io*, fig. 5; *Mx*, fig. 84; Allis 1900 a; 1919 a; 1922; "maxillary-infraorbital", Holmgren and Stensiö 1936, p. 394) is composed of two portions, a tooth-bearing portion with a palatal lamina (*Mx. pal*) and a sensory canal portion, which, as shown by Holmgren and Stensiö, arise separately. Only the tooth-bearing portion will be dealt with here. It is strongly developed in the anterior part below the lachrymal, but becomes weaker backwards and is represented most posteriorly merely by teeth attached to the sensory canal portion. The teeth of the "maxillary" form together with those of the "premaxillary" a continuous row opposed to the row of teeth of the dentary in the lower jaw. As pointed out by Allis (1900 a;

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transverse commissure was developed already in Devonian Coelacanthids. This commissure may thus be an old formation and homologous to the postero-ventro-lateral branch of the supraorbital sensory canal in *Polypterus* that is enclosed in the terminal (cf. p. 602).

1919 a) and SEWERTZOFF (1925), the "maxillary" in *Polypterus* (or more correctly its tooth-bearing portion) is not situated, as in Actinopterygians (*Amia*, *Lepidosteus*, Teleosts), in the maxillary labial fold (plica oralis superior) but medially to that fold. In Coelacanthids no maxillary has been found so far, not even in the recent *Latimeria* (cf. foot-note on p. 349). In this form all the tooth-bearing dermal bones of the jaws are weakly developed and consist to a large extent of loose tooth-plates only. This is also true of both the dentary ("labial tooth plates" of SMITH's description, 1939, p. 63; *46*, fig 8)[1] and the premaxillary ("rostral dental plates" of SMITH's description, 1939, pp. 68—69; *90*, fig. 10). Since these two bones are well developed in fossil Coelacanthids (fig. 81; STENSIÖ 1937 a, figs. 7, 15; NIELSEN 1936, figs. 14, 15), it is obvious that they have developed regressively in *Latimeria*. The premaxillary in *Latimeria* (cf. p. 349) is represented by three tooth-plates (*Pmx*, fig. 35; SMITH 1939; *90*, fig. 10). In *Latimeria* the elements of the lower jaw opposed to the premaxillary tooth-plates are the dentary tooth-plates (SMITH 1939; *46*, fig. 8), which, however, extend considerably further backwards along the oral margin than the premaxillary tooth-plates.[2] Also in *Nesides* (STENSIÖ 1937 a, fig. 3) the tooth-bearing margin of the dentary seems to have extended further backwards than the tooth-bearing margin of the premaxillary. This cannot be a primitive condition and it is thus to be suspected that maxillary teeth antagonistic to the teeth of the posterior part of the dentary are present, or were at least primarily present, in Coelacanthids. In order to be opposed to the posterior teeth of the dentary these maxillary teeth must have been situated medially to the maxillary fold, at least in *Latimeria* (see SMITH 1939, fig. 10; pls. 11, 14; p. 68). Hence it follows that these teeth had the same position as the tooth-bearing portion of the "maxillary" in *Polypterus*.

The anterior part of the parasphenoid in Coelacanthids very greatly resembles the same part in *Polypterus* both as regards forward extent and shape (*Psph*, figs. 5, 74, 81; ALDINGER 1930, figs. 1, 6; 1931 a, fig. 7; MOY-THOMAS 1937, fig. 4; SMITH 1939, figs. 10, 12, 15, 16; STENSIÖ 1921, fig. 42; 1937 a, figs. 5, 8; pl. 3; pl. 12, fig. 2; WATSON 1921, fig. 4; WESTOLL 1939, fig. 4).

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[1] The bone referred to as the "dentary" by SMITH (1939, p. 58), which according to him "appears to be, at least superficially, partly cartilaginous", is probably an ossification in Meckel's cartilage comparable to the mentomeckelian ossicle or mentomandibulare in *Polypterus* (ALLIS 1922, p. 247; pl. 12, figs. 35, 35 a, 37; pl. 13, figs. 42, 43; HOLMGREN and STENSIÖ 1936, p. 392).

[2] SMITH calls the dentary tooth-plates "labial tooth plates", whereas the tooth-plates that are situated farther in and which actually lie as coronoid elements are wrongly termed "dental plates of the dentary".

The vomer seems to have undergone a regressive development in Coelacanthids, and in *Latimeria* it consists only of a fairly small tooth-bearing plate ("postrostral dental plate", SMITH 1939; *91*, fig. 10). Also in *Polypterus* the vomer is vestigially developed ("subrostral", POLLARD 1892, p. 412; pl. 28, fig. 15; ALLIS 1900 a, pp. 277—278; vomer, LAKJER 1927, pp. 186—188; HOLMGREN and STENSIÖ 1936, p. 397; fig. 296) and reminds of that in *Latimeria*.

Two dermal bones are developed in relation to the foremost part of the palatoquadrate in *Latimeria*, an anterior one and a posterior one. They will here be referred to as the predermopalatine and the dermopalatine respectively.

The predermopalatine was described by SMITH (1939, p. 69; *53″*, fig. 10) as the "dental plate of the prevomer". The whole bone lies underneath the ethmoidal region but covers the lower face of an ossification which was described by SMITH as a "prevomer" (SMITH 1939, p. 80; *53*, fig. 7; pl. 27; see also fig. 83 B in the present work and foot-note 2 on this page), but beyond doubt represents the foremost part of the palatoquadrate.[1] Like the vomer and the dermopalatine the predermopalatine is a tooth-bearing plate and lies in a row with these bones and the ectopterygoid. A predermopalatine may be present also in Devonian Coelacanthids, underneath the area of the lower face of the ethmoidal region situated between the vomeral area (*ar. Vo*, fig. 74 A) and the autopalatine articular facet ($art_{a}Aup$). Since the tooth-bearing dermal bones of the jaws in *Latimeria* are generally reduced (p. 607) and sometimes even secondarily subdivided into several plates, it is possible that this applies also to the dermopalatine. If this is so, the predermopalatine in Coelacanthids is simply a disintegrated anterior part of the dermopalatine. It is of great interest that a correspondingly situated dermal bone, which may also be termed predermopalatine, is found in *Polypterus*. The predermopalatine in this form is the tooth-bearing plate hitherto known as vomer (POLLARD 1892; GOODRICH 1930, fig. 296 B; DE BEER 1937, p. 86), dermopalatine (LAKJER 1927, pp. 186—188; HOLMGREN and STENSIÖ 1936, p. 397), and mesial dermopalatine (ALLIS 1919 a; 1922), and connected with the foremost part of the palatoquadrate. Correlative with the weak development of the vomer it extends far forwards underneath the ethmoidal region and conceals the palatal processes of the "maxillary" and the "premaxillary" (*Mx. pal*, *Pmx. pal*, fig. 5 B). Posteriorly it is attached to the dermopalatine.[2]

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[1] Judging from SMITH's description, the "prevomer" seems to be a separate ossification in the palatoquadrate immediately antero-medially to the autopalatine ossification.

[2] In *Latimeria* the palatoquadrate extends fairly far antero-medially beyond its articulation with the ethmoidal region and thus has a prearticular autopalatine part, the

The dermopalatine both in *Latimeria* ("autopalatine dental plate", Smith 1939, pp. 69—70; *37''*, fig. 10) and *Polypterus* (Allis 1922, pl. 9, figs. 24, 26; pl. 10, figs. 29, 30; Goodrich 1930, fig. 296 B) is situated behind the predermopalatine. In *Polypterus* it is fused with the ectopterygoid (Allis 1922, p. 244; De Beer 1937, p. 86).

The above comparison reveals that as regards the development of the snout the Coelacanthids agree in several characters with *Polypterus*. The most important of these characters may be summarized as follows.

1) The general development of the divisio prenasalis communis. The presence of a dorsal and a ventral rostral process separated by a transverse groove for the ethmoidal commissure of the infraorbital sensory canals. The absence in this divisiόn of the ethmoidal region of cavities and large canals for nerves and vessels.

2) The agreement in the general proportions of the internasal wall and the shape and position of the median rostral cavity between Coelacanthids and larvae of *Polypterus*, in which the foremost part of the cranial cavity (corresponding to the median rostral cavity) extends forwards between the nasal cavities.

3) The complete development of the nasal walls.

4) The presence of a fenestra endonarina communis and the position and shape of that fenestra.

5) The absence of a fenestra endochoanalis and a choana.

6) The presence of an antero-medial recess in the nasal cavity, occupied by an antero-medial diverticle of the nasal sac.

7) The development of the canalis olfactorius, which consists of a posterior long and high part and an anterior shorter and narrower part, indicating that the bulbus olfactorius was long and high and the olfactory nerve comparatively short.

8) The development of the foremost part of the cranial cavity, which may imply that the forebrain was *Polypterus*-like.

9) The presence of a canal, presumably for an orbitonasal artery, running from the ventro-medial part of the orbit to the canalis olfactorius.

"prevomer" of Smith's description. It is uncertain whether in *Polypterus* the pars autopalatina of the palatoquadrate has a corresponding prearticular part. Pollard (1892, pp. 418, 419; pl. 29, fig. 20; pl. 30, fig. 34) says, however, that the palatoquadrate in *Polypterus* has an anterior continuation, the "prearticular prolongation" or "prepalatine bar", in front of the articular connection with the endocranium. If this "prearticular prolongation" actually exists (cf. Allis 1922, p. 244; Lakjer 1927, p. 188), it must lie ventrally to the cartilaginous area of the lower face of the ethmoidal region that is situated immediately antero-medially to the articular area of the autopalatine (*art. aup*, fig. 5; the area denoted *End. cart* on the left side of fig. 5 B). This "prearticular prolongation" of the palatoquadrate would thus be situated somewhat as the prearticular autopalatine part of the palatoquadrate in *Latimeria*.

10) The fact that the n. profundus is represented by the ventral branch (cf. p. 268), which ramified in a similar way as in *Polypterus* and entered the nasal cavity.

11) The fact that the r. ophthalmicus lateralis seems to have been accompanied in the ethmoidal region by an a. ophthalmica and a v. ophthalmica. The latter is formed by the union of two branches from the anterior parts of the snout, one lateral and one medial, and receives in the anterior part of the orbit two tributaries coming from the cranial cavity, the posterior one in company with or close to the n. trochlearis.

12) The fact that the r. buccalis lateralis, presumably accompanied by the r. maxillaris V, the a. maxillaris and the v. infraorbitalis, entered the nasal cavity either at the postero-ventral corner of the fenestra endonarina communis, as in larvae of *Polypterus*, or, as in adults of *Polypterus*, through the lateral nasal wall a little behind the fenestra endonarina communis.

13) The places of origin of the mm. obliqui of the eye and the presence of a distinct dorsal anterior myodome.

14) The absence of an intermaxillary gland and of all structures developed in relation to such a gland.

15) The presence of paired ethmoidal and autopalatine ossifications.

16) The position and development of the articulation of the palatoquadrate with the ethmoidal region, and presumably also the presence of a prearticular autopalatine part in the palatoquadrate.

17) The relatively high position of the infraorbital sensory canal in the hinder part of the snout and the fact that it crosses the ventral part of the fenestra endonarina communis.

18) The course of the supraorbital sensory canal, which anastomoses anteriorly with the infraorbital canal antero-medially to the anterior external nostril and anteriorly gives off a postero-ventro-laterally directed branch (the anterior transverse commissure) running close behind the anterior external nostril.

19) The development of the dermal bones connected with the anterior part of the infraorbital canal, i. e. the anterior part of the lachrymo-jugal, the lateral rostral and the medial rostrals. These bones are fundamentally as the lachrymal and the sensory canal components of the complex "premaxillary" and median rostral in *Polypterus*.

20) The presence of two nasal elements in certain Coelacanthids, as in *Polypterus*, a comparatively small anterior one and a larger posterior one.

21) The presence of an antero-dorsal process of the lateral rostral developed in connection with a comissure issuing from the foremost part of the supraorbital canal and probably corresponding to the postero-ventro-lateral branch of the supraorbital canal in *Polypterus*. The antero-dorsal

process of the lateral rostral also has exactly the same position in relation to the endocranium, nostrils and nasal tubes as the terminal bone in *Polypterus*, and seems to be the homologue of that bone.

22) The narrow shape of the postrostrals in Coelacanthids like that of the presumed postrostral component of the median rostral in *Polypterus*.

23) The position and extent of the posterior tectal, corresponding to the position and extent of the probably homologous postero-dorsal facial portion of the complex "premaxillary" in *Polypterus*.

24) The position and extent of the premaxillary, identical with those of the tooth-bearing component of the complex "premaxillary" in *Polypterus*.

25) The fact that the maxillary, if developed, would have been situated as the maxillary component of the maxillo-jugal in *Polypterus*.

26) The forward extent and shape of the anterior part of the parasphenoid.

27) The position and development of the vomer.

28) The presence, position and extent of the predermopalatine.

There are also certain differences in the snout between Coelacanthids and *Polypterus*, but they seem to be of little importance. The following differences may be mentioned here.

1) The n. profundus in fossil Coelacanthids did not accompany the r. ophthalmicus lateralis forwards from the orbit, as it does in *Polypterus*, but pierced the postnasal wall lower down in a separate canal. This is probably a primitive condition in Coelacanthids. That the n. profundus in *Polypterus* in certain cases passes ventrally to the m. obliquus superior, as it must have done in Coelacanthids, whereas in other cases it goes dorsally to the said muscle, may indicate that its dorsal position in *Polypterus* is secondary and due to the absence in adults of the embryonic ethmoidal part of the cranial cavity.

2) The posterior external nasal tube opens outwards with two nostrils in Coelacanthids, but with a single one only in *Polypterus*. In this respect Coelacanthids are certainly more specialized than *Polypterus*. On the other hand their posterior nasal tube is enclosed in a canal in the anterior part of the posterior tectal, and in this respect they are probably more primitive than *Polypterus*.

3) The fusions of the dermal bones of the snout have taken place in a somewhat different way in Coelacanthids and *Polypterus*. In Coelacanthids the premaxillary, the medial rostrals, the posterior tectal and the postrostrals are all independent. The lateral rostral seems to have fused with an anterior tectal, which latter forms the antero-dorsal process. In *Polypterus* the corresponding tectal element may be independent and forms the terminal bone. In *Polypterus* the premaxillary, the middle

and the lateral of the medial rostrals, the lateral rostral and the posterior tectal have fused into a large complex bone which should properly be termed tecto-rostro-premaxillary. The most medial one of the medial rostrals has fused with the corresponding one of the opposite side, and possibly also with the postrostrals, to a compound median rostral or perhaps rostro-postrostral.

4) In Coelacanthids the dermal bones of the ethmoidal shield are devoid of palatal processes. In *Polypterus* both the "maxillary" and the "premaxillary" are provided with large palatal laminae, but these are probably secondary formations.

Certain of the common characters in the snout of Coelacanthids and *Polypterus* are clearly of little importance or are primitive ones, but several are beyond doubt of a more profound nature and cannot possibly be mere parallelisms. Also in the other parts of the head Coelacanthids present several remarkable points of agreement with *Polypterus*. On the other hand, they also differ strongly from *Polypterus*, e. g. in the fins and their skeleton and in the structure of the scales[1]. Some facts thus favour the belief that Coelacanthids and *Polypterus* are closely related whereas others decidedly contradict this. In these circumstances it seems most reasonable to assume that the more fundamental characters in which Coelacanthids and *Polypterus* agree are on the whole primitive ones inherited from some common ancestral form. Be this as it may, however, Coelacanthids and *Polypterus* are more similar than has generally been assumed, particularly during the past few decades (GOODRICH 1924; 1928; 1930; ROMER 1933, pp. 76—77; MOY-THOMAS 1933; 1934; 1939 a, pp. 117, 132; SÄVE-SÖDERBERGH 1934; GROSS 1935; WESTOLL 1937, p. 373; 1937 b, p. 570; BERG 1937; 1940; 1940 a; ALDINGER 1937, p. 377; E. I. WHITE 1939, p. 60, and others). In view of what has been shown above and for several other reasons (cf. the following chapter) *Polypterus* and *Calamoichthys* cannot possibly be regarded as Actinopterygians but must represent a group of their own. For this group I have retained the name *Brachiopterygii* suggested by STENSIÖ (1921, p. 147).

d. Comparison with Actinopterygians.

Coelacanthids — and also Brachiopterygians (*Polypterus*) — have several characters in common with Actinopterygians. The following deserve to be mentioned here.

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[1] This according to GOODRICH (1907; 1909, p. 292; 1928; cf. GROSS 1935; MOY-THOMAS 1937, p. 397; ALDINGER 1937, pp. 214—215, 227—229, 371—373, 380—381) who maintains that the scales of *Polypterus* are of the ganoid type, whereas those of Crossopterygians belong to the cosmoid type. MATVEYEV (1940, p. 651), on the other hand, states that "the structure of the bony scales of *Polypteri* is very similar to the type of cosmoid scales of *Osteolepidae*".

1) The general tendency to develop a paired ossification in the hinder part of the ethmoidal region (cf. No. 24, p. 595). In *Palaeonisciformes* the ethmoidal ossification is unpaired, as in the geologically oldest Coelacanthids (WATSON 1928, p. 62; DYNE 1939, p. 207). The presence of a preethmoid (*Pe*, fig. 10 C, D) in certain Actinopterygians is certainly due to special conditions, above all to the great mobility of the whole upper jaw apparatus.

2) The presence of an autopalatine ossification in the palatoquadrate (*Aup*, figs. 5 A, 9, 77 B, C, 80—83; HOLMGREN and STENSIÖ 1936, pp. 409, 424, 457, 492).

3) The complete development of the solum nasi. The absence of a fenestra endochoanalis and a choana.

4) The fusion of the fenestra endonarina anterior and fenestra endonarina posterior into a fenestra endonarina communis. Since the nasal cavity in Actinopterygians generally has no roof and likewise to a large extent lacks a lateral wall, the fenestra endonarina communis is as a rule a very large opening, often devoid of definite boundaries anteriorly, dorsally and laterally. Typical *Palaeonisciformes* appear to lack the tectum nasi and prenasal wall (WATSON 1925, pp. 843—844; figs. 10—13, 18; CASE 1937; DYNE 1939, p. 207; EATON 1939 a; NIELSEN 1942), and one might thus be inclined to believe that this was a primitive condition in Actinopterygians. However, both the prenasal wall and the tectum nasi are well developed in *Australosomus* (PIVETEAU 1934, fig. 6), *Saurichthys* (STENSIÖ 1925, figs. 1, 16 A, 39; 1932, figs. 28 A, 33) and sturgeons (fig. 10 A), and this possibly implies that the development of the nasal capsules in primitive Actinopterygians was approximately as complete as in Coelacanthids and Brachiopterygians.

5) The fact that the anterior and posterior external nasal tubes open outwards through anterior and posterior nostrils situated on the lateral side of the snout. It is worthy of notice, however, that in typical *Palaeonisciformes* the posterior nasal tube went backwards to and had its posterior orifice (the posterior external nostril) in the foremost part of the orbital opening (cf. *fe. exa*, fig. 85). The posterior external nasal tube in these forms thus had the same extent as the nasolachrymal duct in *Eusthenopteron* and Amphibians, and this relation of the posterior external nasal tube to the eye may therefore be suspected to be a primitive feature. Be this as it may, it is very desirable that special attention be paid to the relations of the posterior nasal tube in primitive Actinopterygians.

6) The forward extension of the palatoquadrate far underneath the ethmoidal region and its articulation (as a rule) with the lower face of that region (*art. aup*, fig. 5 B, *art*$_a$*Aup*, fig. 74; ALLIS 1898, pl. 33, fig. 6;

Holmgren and Stensiö 1936, *fac. art. pal*, fig. 320 B). It should be mentioned, however, that in connection with the specialization of the upper jaw apparatus in Actinopterygians the articulation between the palatoquadrate and the ethmoidal region has often become highly modified.

7) The uniting of the r. maxillaris V and the r. buccalis lateralis into a truncus infraorbitalis (*r. mx + buc*) both in *Polypterus* (fig. 9) and Actinopterygians (fig. 10 D) and probably also in Coelacanthids (fig. 78 B).

8) The general trend to develop anterior myodomes for the mm. obliqui of the eye.

9) The course of the infraorbital sensory canal decidedly laterally to the postnasal wall. In Ganoids and Teleosts the infraorbital canal as a rule runs laterally to the ventral part of the postnasal wall and at least in several higher Ganoids (*Amia*, Allis 1889; pl. 34; pl. 41, fig. 45; pl. 42; Pehrson 1922, figs. 16, 17; 1940, figs. 2, 5, 6, 13, 14, 28; *Sinamia*, Stensiö 1935, fig. 19; *Lepidosteus*, Allis 1904, pl. 8, fig. 2 a; Hammarberg 1937, fig. 40; *Lepidotus*, Holmgren and Stensiö 1936, fig. 365) it makes a more or less distinct dorsal curve in this part of its course in the same way as in *Polypterus* (fig. 84) and Coelacanthids (fig. 77 A, B; cf. pp. 334—335 and figs. 40 B, 41, 52 B, 53, 58, 68 A, 71 A). In this connection it should also be mentioned that in Actinopterygians, as in *Porolepiformes*, *Osteolepiformes*, Coelacanthids and Brachiopterygians, the infraorbital canals form an ethmoidal commissure (in Teleosts generally represented by a pit-line; cf. p. 279 and foot-note 1 on p. 258).

10) The primary fundamental pattern of the dermal bones developed in relation to the anterior part of the infraorbital sensory canal. The infraorbital sensory canal pierces a series of rostral elements in the snout, easily comparable to that in *Polypterus*, Coelacanthids and Rhipidistid Crossopterygians (cf. Stensiö 1921, pp. 274—277; Pehrson 1922, 1940; Holmgren and Stensiö 1936, pp. 410, 420, 421, 441—442, 459). A closer analysis of the dermal bones of the dorsal side of the snout also reveals, as will be seen below (pp. 615—619), that the primary general pattern of the existing dermal bones of the snout in Actinopterygians probably is not so fundamentally different from that in Brachiopterygians, Coelacanthids and Rhipidistid Crossopterygians as one might perhaps be inclined to believe.

The main features in the snout of Coelacanthids and Brachiopterygians different to those of Actinopterygians are as follows.

1) The presence of an antero-medial recess in the nasal cavity, occupied by an antero-medial diverticle of the nasal sac. (As has been pointed out above, p. 266, the mucous membrane of the nasal sac in *Polypterus* is folded in quite a different way to what it is in Actinopterygians).

2) The presence of the ventral branch only (r. ophthalmicus profundus or r. nasalis) of the n. profundus in the snout of Coelacanthids, as in that of *Polypterus.* In Actinopterygians it is instead the dorsal branch of the nerve (the r. frontalis or portio ophthalmici profundi) that is most strongly developed and supplies the snout (cf. pp. 253, 254, 263 foot-note 1, 268).

3) The fact that the truncus infraorbitalis, presumably accompanied by vessels, entered the nasal cavity (figs. 9, 78 B, 79; cf. Stensiö 1932, *s. max. buc*, fig. 33).

4) The presence of a special canal (for the orbitonasal artery) passing from the orbit to the canalis olfactorius. In Actinopterygians there is no corresponding canal or artery.

5) The origin of the m. obliquus inferior far ventrally and far below the m. obliquus superior (figs. 9, 78 B). In Actinopterygians the mm. obliqui of the eye seem at least as a rule to arise close to one another, and several Actinopterygians have a common anterior myodome for these muscles (fig. 10 D; cf. Holmgren and Stensiö 1936, p. 486).

6) The presence of a predermopalatine.

7) The anastomosis of the supraorbital sensory canal with the infraorbital one (as in Rhipidistid Crossopterygians) close to the tip of the snout, antero-medially to the anterior external nostril. No corresponding anastomosis exists in Actinopterygians. As already pointed out above (p. 346), the sensory canal in lower Actinopterygians, generally regarded as the foremost part of the supraorbital canal, has a position in relation to the ethmoidal region and the external nostrils quite different to that of the foremost part of the supraorbital sensory canal in Crossopterygians (and Brachiopterygians) and can hardly be homologous to that (see below). In Actinopterygians the dermal bones on the upper side of the snout, the rostrals excepted, are highly influenced by this special development of the sensory canal system and are not easily comparable to the correspondingly situated dermal bones in Crossopterygians and Brachiopterygians.

In the vast majority of lower Actinopterygians which may be referred to as the *Palaeonisciformes* (Hay 1929) the sensory canal system and the dermal bones of the dorsal side of the snout are on the whole very uniform (fig. 85; Traquair 1877—1914; Stensiö 1921; 1932; Watson 1925; 1928; Moy-Thomas 1934; 1939 a; Piveteau 1934; Holmgren and Stensiö 1936; Aldinger 1937; Westoll 1937 b; Moy-Thomas and Dyne 1938; Dunkle 1939; Dyne 1939; E. I. White 1939; Berg 1940; Nielsen 1942; etc.). After leaving the frontal the supraorbital sensory canal (*soc, socp*, fig. 85) turns sharply laterally and downwards and connects with the infraorbital canal on the lower posterior part of the lateral side of the snout. The ventro-laterally descending portion of the supraorbital canal pierces a high bone, generally termed the nasal (*Na*, fig. 85), which forms the anterior margin of the orbital opening. This bone separates the fenestra exonarina anterior (*fe. exa*) from the fenestra exonarina posterior (*fe. exp*). The fenestra exonarina anterior is bounded by the "nasal" and a median bone in front, the postrostral (*Ptr*), whereas the fenestra exonarina posterior is represented by a notch in the orbital margin of the "nasal". The lower part of the preorbital ventro-laterally curving part of the supraorbital canal was thus situated between the anterior and posterior external nostrils. The postrostral (*Ptr*) is unpaired and as a rule represented by a single plate only. In addition to the bones mentioned several rostral elements, the premaxillaries and the maxillaries are also found in the snout of *Palaeonisciformes*.

The ventral part of the ventro-laterally curving portion of the supraorbital sensory canal in *Palaeonisciformes* as well as Saurichthyids (Stensiö 1925; 1932, pp. 115—116; Holmgren und Stensiö 1936, figs. 323, 324) and sturgeons (Allis 1904) previously considered to be the rostral part of the supraorbital sensory canal and situated laterally to the postnasal wall and the posterior part of the nasal cavity, cannot possibly be the equivalent of the foremost part of the supraorbital canal in *Polypterus*, Coelacanthids and Rhipidistid Crossopterygians which is situated dorsally to the divisio prenasalis communis and is connected with the infraorbital canal antero-medially to the anterior external nostril (figs. 32—35, 84; cf. pp. 345—346). Consequently the ventralmost part of the so-called nasal between the anterior and posterior external nostrils in *Palaeonisciformes* cannot possibly correspond to the anterior nasals in *Polypterus* and Crossopterygians but must be of a different nature.

The sensory canals and dermal bones of the snout are thus to a large extent developed differently in Brachiopterygians and Crossopterygians to what they are in *Palaeonisciformes*, Saurichthyids and sturgeons. This and the fact that the snout in *Polypterus* is very similar to that in Coelacanthids strongly contradicts the current opinion that *Polypterus* belongs or is closely related to the *Palaeonisciformes* (Goodrich 1928; Moy-Thomas 1933; 1934; 1939 a, pp. 106, 127, 132; Aldinger 1937, pp. 377, 379; Westoll 1937, p. 373; 1937 b, p. 570; Berg 1940; 1940 a and others). On the other hand it is obvious that in certain respects, e. g. in the structure of the brain and the paired fins and possibly also of the scales (see Goodrich 1928; cf. foot-note 1, p. 612), *Polypterus* decidedly approaches the Actinopterygians and is thus intermediate between Crossopterygians and Actinopterygians. There is therefore reason to believe that the sensory canals and dermal bones of the dorsal side of the snout in Actinopterygians may have arisen through modifications of dermal bones and sensory canals with a corresponding fundamental

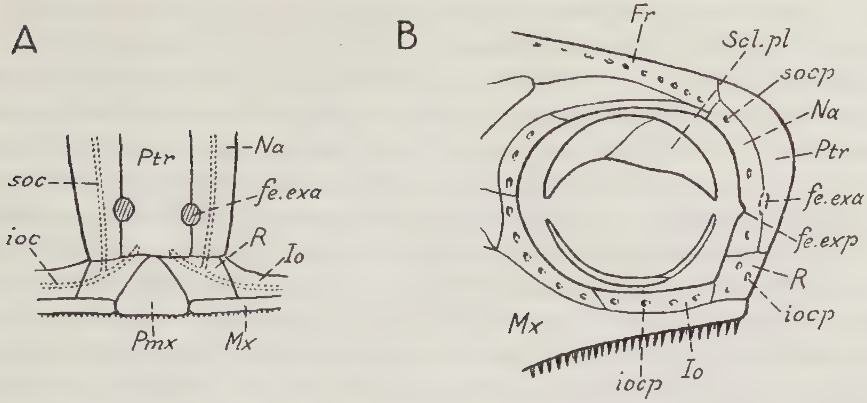

Fig. 85. The dermal bones and sensory canals of the snout in two *Palaeonisciformes*. The terminology is the one currently used for this group. *A*, *Canobius ramsayi* Traquair. Anterior view. From MOY-THOMAS and DYNE (1938, fig. 40). *B*, *Cornuboniscus budensis* White. Lateral view. From E. I. WHITE (1939, fig. 1 C).

Fr, frontal; *Io*, infraorbital; *Mx*, maxillary; *Na*, "nasal"; *Pmx*, "premaxillary" or "dentigerous rostral"; *Ptr*, postrostral; *R*, rostral; *Scl.pl*, sclerotic plates; *fe.exa*, fenestra exonarina anterior; *fe.exp*, notch representing fenestra exonarina posterior; *ioc*, *iocp*, infraorbital sensory canal and pores; *soc*, *socp*, supraorbital sensory canal and pores.

disposition as in Crossopterygians and Brachiopterygians. That this actually is so is difficult to prove with the very imperfect knowledge that we still have of the sensory canal system and the dermal bones of the earliest and most primitive Actinopterygians. An attempt is made below, however, to give what is partly a new interpretation of the sensory canals and dermal bones on the dorsal side of the snout in Actinopterygians.

In the fossil Amiid *Sinamia* (STENSIÖ 1935, figs. 18, 19) there are between the anterior and posterior external nostrils two transverse commissural sensory canals, anterior and posterior, connecting the supraorbital and infraorbital canals. The same commissures are present also in *Amia* (ALLIS 1889; PEHRSON 1922, fig. 16; 1940, figs. 1, 2, 5—8, 13, 14, 27, 28) but here the anterior one is vestigial, being represented by the foremost laterally bent portion of the supraorbital sensory canal that lies close behind the anterior external nostril in the antero-lateral part of the so-called nasal and lodges organ 1 of the supraorbital sensory canal. The ventral part of the posterior commissure in *Amia* lies in the postero-dorsal part of the so-called antorbital and lodges organ 5 of the infraorbital sensory canal. These commissures in *Sinamia* and *Amia* agree very well in position and course with the anterior and posterior transverse commissures in Coelacanthids (*com. tra*, *com. trp*, figs. 32, 35). Of these latter the anterior one belongs to the supraorbital sensory canal, as proved by conditions in the undetermined Triassic Coelacanthid preliminarily described by NIELSEN (fig. 32 B), whereas the posterior one is at least very likely developed from the infraorbital sensory canal (cf. fig. 32 A and p. 336), thus exactly as in *Amia*. On account of these great similarities, on account of the presence in *Polypterus* of an anterior transverse commissure apparently homologous to that in Coelacanthids (cf. p. 602, foot-note 1 on p. 605), and on account of the points of agreement between Coelacanthids, *Polypterus* and Actinopterygians demonstrated above (pp. 612—614), it seems reasonable to assume that the correspondingly situated commissures in *Sinamia* and *Amia* and Coelacanthids are homologous. If they are, it is evident that the sensory canal system of the snout in *Sinamia* and *Amia* is essentially as in Coelacanthids, the main difference being that the supraorbital canal in them does not join the infraorbital canal at the tip of the snout anteromedially to the anterior external nostril.

If we presume that the above homologations are correct, the dermal bones on the dorsal side of the snout in *Amia* may be interpreted as follows (these interpretations are based mainly on the disposition of the dermal bones of the snout in Coelacanthids and on Pehrson's embryological investigations of the development of the dermal bones in *Amia*). The infraorbital canal pierces a rostral series consisting of a lateral rostral formed by the part of the so-called antorbital that encloses the sensory canal organs 3, 4 and 6 of the infraorbital canal (see Allis 1889, pl. 42; Pehrson 1922, fig. 16; 1940, figs. 2, 5, 6, 13, 14) and two medial rostrals fused with one another and with those of the opposite side into a complex median rostral (Pehrson 1940, pp. 9—10, figs. 10, 27). Dorsomedially to the rostral series we may distinguish a tectal series, composed of three elements, posterior, middle and anterior. The posterior tectal element is the so-called dermectethmoid (*Dece*, fig. 10 C, D; cf. Holmgren and Stensiö 1936, p. 454). This element probably corresponds to the posterior tectal (*Te.p*, figs. 35, 77 A) in Coelacanthids and to the postero-dorsal facial portion (*Pmx.fa*, figs. 5, 84) of the complex "premaxillary" in *Polypterus* (cf. p. 606). The middle element is represented by the part of the so-called antorbital that is pierced by the ventral part of the posterior transverse commissure and lodges organ 5 of the infraorbital canal (Pehrson 1940, figs. 2, 5, 6, 13, 14). This element seems to correspond to the hindmost of the anterior tectals (bone No. *5* in fig. 35) in *Latimeria*, which is also developed in connection with the posterior transverse commissure (*com. trp*). The anterior tectal element is the antero-lateral part of the so-called nasal which houses the vestigial anterior transverse commissure. This part arises independently (Pehrson 1922, fig. 16; 1940, figs. 1, 2, 6—8, 13, 14) and is possibly the homologue of the terminal in *Polypterus* (*Term*, fig. 84) and the antero-dorsal process (*pr. R. l*, figs. 35, 77 B, 80) of the lateral rostral in Coelacanthids (cf. pp. 605—606). The nasal series consists of two elements, as in *Polypterus* and certain Coelacanthids (*Mylacanthus* or *Scleracanthus*?, cf. p. 606). These elements fuse with each other and with that interpreted as the anterior tectal element. The so-called nasal in the adult *Amia* would thus be a complex tecto-nasal, and the so-called antorbital, which seems to include the lateral rostral and the middle tectal element, would be a complex rostro-tectal. *Amia* is devoid of postrostrals, but their absence is presumably secondary, for one or two postrostrals are found in lower Ganoids (*Ptr*, fig. 85; WATSON 1925, figs. 1—3; HOLMGREN and STENSIÖ 1936, p. 410; cf. PIVETEAU 1934, fig. 51), and in advanced Coelacanthids (*Axelia*, *Mylacanthus* or *Scleracanthus*?, STENSIÖ 1921; *Ir*, figs. 43, 51; the unnamed Triassic form described by NIELSEN, 1936; *R*, *Ir*, fig. 10, and *Latimeria*; *Ptr*, fig. 35; cf. foot-note 1, p. 352) the postrostrals are much reduced.

The above analysis of the sensory canals and the dermal bones of the upper side of the snout in *Amia* may perhaps throw some light upon the conditions in *Palaeonisciformes* and other lower Ganoids. It is thus not difficult to see that the ventro-laterally running preorbital portion of the supraorbital sensory canal in *Palaeonisciformes* (fig. 85) in its lower part, situated behind the fenestra exonarina anterior, is essentially as the anterior transverse commissure between the infraorbital and supraorbital canals in *Amia*, *Sinamia*, *Polypterus*, and Coelacanthids. From this follows that the ventral part of the "nasal" in *Palaeonisciformes* probably includes a tectal element and is a tecto-nasal. A posterior transverse commissure suggestive of that in Coelacanthids, *Amia* and *Sinamia* seems also to be present at least in certain *Palaeonisciformes* such as *Cheirolepis* (WATSON 1925, fig. 3) and *Birgeria* (STENSIÖ 1932, fig. 41). In *Birgeria* the commissure ascends in a dorsal process from the posterior part of the bone that STENSIÖ has termed "antorbital". The "antorbital" in *Birgeria* is in all respects as the "antorbital" in *Amia* (cf. HAMMARBERG 1937, pp. 290—292) and like that bone in *Amia* probably includes a tectal element and is a rostro-tectal.

As may be gathered from the above, Coelacanthids have several general primitive characters in common with Actinopterygians. Coelacanthids are on the whole much more similar to Actinopterygians than are *Porolepiformes* and *Osteolepiformes*. The fact that Coelacanthids and Actinopterygians clearly approach each other as regards the snout and that the primitive general disposition of the dermal bones in the head of Crossopterygians and Actinopterygians may have been very similar indicates that there probably is not so wide a gap between Crossopterygians and Actinopterygians as earlier assumed.

e. Comparison with Dipnoi.

Coelacanthids and Dipnoans show inter alia the following differences in the structure of the snout. 1) The ethmoidal region is as a whole much more strongly and completely developed in Coelacanthids than in Dipnoans. 2) The internasal wall in Coelacanthids houses a closed space, the median rostral cavity, which has no equivalent in Dipnoans. 3) The postnasal wall is very strongly developed in Coelacanthids, whereas in Dipnoans it is much reduced. 4) The solum nasi is complete in Coelacanthids, but entirely reduced in Dipnoans. 5) In Coelacanthids the fenestra endonarina anterior and the fenestra endonarina posterior are fused into a fenestra endonarina communis; in Dipnoans the fenestra endonarina anterior and the fenestra endonarina posterior are separated from one another by a cartilage, the subnasal cartilage, which is a part of the lateral nasal wall. 6) The fenestra endonarina communis in Coelacanthids lies on the lateral side of the snout; the fenestra endonarina anterior and the fenestra endonarina posterior in Dipnoans are situated ventrally to the nasal sac in the roof of the mouth. Owing to this the very short posterior nasal tube in Dipnoans opens into the mouth cavity and is developed as a pseudo-choana. The long posterior external nasal tube in Coelacanthids, on the other hand, opens outwards on the lateral side of the snout not very far in front of the eye. 7) There are two posterior external nostrils in Coelacanthids, but only one in Dipnoans. 8) The nasal sac is provided with an antero-medial diverticle in Coelacanthids, but not in Dipnoans. 9) The r. maxillaris V and the r. buccalis lateralis in Coelacanthids were probably united into a truncus infraorbitalis which entered the nasal cavity; the corresponding nerves in Dipnoans are not intimately united and do not enter the nasal cavity. 10) The bulbus olfactorius is developed in a different way in Coelacanthids and in recent *Dipnoi.* 11) The infraorbital sensory canals meet in an ethmoidal commissure in Coelacanthids, but not in Dipnoans. 12) In Coelacanthids the anterior end of the supraorbital sensory canal anastomoses with the infraorbital canal near the tip of the snout. 13) In Coelacanthids there are an anterior and a posterior transverse commissure between the infraorbital and supraorbital canals; in Dipnoans there are no such commissures; 14) The palatoquadrate in Coelacanthids is independent; in Dipnoans it is fused with the endocranium, and the dermal bones of the palate are of a very special type.

Thus, the Coelacanthids differ very considerably from Dipnoans in the structure of the snout. It may be emphasized, however, that most of the differences are certainly due to secondary modifications in the

Dipnoans in connection with the transformation of the dentition into tritoral plates, the fusion of the palatoquadrate with the endocranium and the migration of the nostrils to the lower side of the snout.

f. Comparison with Urodela and Anura.

As regards the snout Coelacanthids differ from Urodeles and Anurans in fundamentally the same characters as from *Porolepiformes* and *Osteolepiformes* respectively. For the differences between Coelacanthids on the one hand and Urodeles and Anurans on the other the reader is referred to the chapter "Comparison with *Porolepiformes* and *Osteolepiformes*" (pp. 593—597).

V. Remarks on the snout in Stegocephalians.

According to current opinions (DOLLO 1895; BAUR 1896; WOODWARD 1898; GREGORY 1915; 1920; 1929; 1931; WATSON 1919; 1926; 1940; FRANZ 1924; 1931; SEWERTZOFF 1926 a; WERNER 1930—1931; VERSLUYS 1931; NOBLE 1931; SÄVE-SÖDERBERGH 1932 a; 1933 a; 1934; 1935; 1936; ROMER 1933; 1937; 1941; CASE 1933; DEMPSTER 1935; HERRE 1935; v. HUENE 1936; 1936 a; 1940; PIVETEAU 1937; WESTOLL 1938; 1938 a; KUHN 1938; 1939; MOY-THOMAS 1939 a; T. E. WHITE 1939; PARRINGTON and WESTOLL 1940, and others; cf. STADTMÜLLER 1936, pp. 505—513) Stegocephalians have evolved from Crossopterygians or from ancestors closely allied to Crossopterygians. They are also generally considered to have given rise to all other Tetrapods. In the preceding chapters it has been shown that Urodeles must be derived from Porolepiform Crossopterygians (p. 422), whereas Anurans must be descendents of Osteolepiform Crossopterygians (p. 551). It has thus been found that Urodeles and Anurans have arisen independently of each other from two different groups of Crossopterygians. If it is true, as generally maintained, that the Tetrapods have passed through a Stegocephalian stage, we must therefore expect the Stegocephalians to include forms transitional both between Porolepiform Crossopterygians and Urodeles and between Osteolepiform Crossopterygians and Anurans. The snout differs in several fundamental characters in the two lineages *Porolepiformes—Urodela* and *Osteolepiformes—Anura.* If only we had a fair knowledge of the structure of their snout, it would thus be pretty easy to refer the various types of Stegocephalians to one or other of these two lineages. However, only the dermal bones are preserved of the snout in Stegocephalians. Since, as shown above

(p. 353), the majority of the dermal bones of the snout agree in all essentials in *Porolepiformes* and *Osteolepiformes,* we cannot generally with the help of these bones exclusively make out whether a Stegocephalian belongs to the *Porolepiformes—Urodela* lineage or to the *Osteolepiformes—Anura* lineage. Certain of the dermal bones of the snout, however, present considerable differences in *Porolepiformes* and *Osteolepiformes.* This is above all true of the lateral rostral, which in *Osteolepiformes* is provided with a process, the processus dermintermedius, extending inwards into the nasal cavity and corresponding to the septomaxillary in Anurans. Also the dermal bones of the palate are clearly differently developed in *Porolepiformes* and *Osteolepiformes.* When the lateral rostral and the dermal bones of the palate are preserved, we are therefore able to judge with some probability whether we are concerned with forms of the *Porolepiformes—Urodela* lineage or with representatives of the *Osteolepiformes—Anura* lineage. In these circumstances we shall here deal with the Stegocephalians particularly with reference to the lateral rostral and the dermal bones of the palate.

The Ichthyostegids, the oldest known Stegocephalians (Säve-Söderbergh 1932 a), differ from Crossopterygians, other Stegocephalians and modern Amphibians inter alia in the position of the external nostril ventrally to the skull-roof between the posterior tooth-bearing part of the naso-rostro-premaxillary and the anterior end of the maxillary. In the light of our present increased knowledge of the passage of the external nasal tubes through the exoskeleton in lower Gnathostomes, the opening in the exoskeleton in Ichthyostegids that transmitted the external nasal tube clearly seems to represent the fenestra exonarina anterior in Crossopterygians. From this it follows that the anterior nostril in Ichthyostegids was an anterior external nostril strictly homologous to the anterior external nostril in other Tetrapods. If the Ichthyostegids actually have arisen from Crossopterygian ancestors, which there is strong reason to believe that they have, their external nostril must have shifted downwards from a primarily lateral position, and the ventral position cannot possibly be a primary condition as maintained by Säve-Söderbergh (1932 a, pp. 98—99).

As a result of the secondary ventral position of the fenestra exonarina anterior and the external nostril the lateral rostral in Ichthyostegids was pushed so far downwards and medially towards the mouth cavity that it was probably entirely reduced. There is therefore presumably no lateral rostral in Ichthyostegids, the infraorbital sensory canal passing forwards from the lachrymal to the naso-rostro-premaxillary in the skin ventro-medially to the fenestra exonarina anterior (see Säve-Söderbergh 1932 a, fig. 8).

The dermal bone forming the dorsal boundary of the fenestra exonarina anterior in Ichthyostegids is undoubtedly, as assumed by Säve-Söderbergh, homologous to the anterior tectal ("anterior antorbital") — or anterior tectals — in Crossopterygians (*Te. a*, figs. 33—35, 68 A; pp. 351, 415, 448, 549), but it cannot represent either the septomaxillary in Anurans, which, as we have seen (pp. 529—535), is primarily a process (the processus dermintermedius) of the lateral rostral, or the so-called septomaxillary in Urodeles, which, as we now know (pp. 249, 293—295, 402, 422), is a cartilage-bone, the nariodal, in the lateral nasal wall (cf. Säve-Söderbergh 1932 a, pp. 101—102; Jarvik 1937, p. 122).

The septomaxillary is known in numerous Postdevonian Stegocephalians (cf. Säve-Söderbergh 1932 a, pp. 101—102; 1935, pp. 33—38; figs. 2, 5, 7, 10, 12, 13, 14, 21, 60—64, 67), e. g. *Eugyrinus* (Watson 1940, p. 215; fig. 12), *Miobatrachus* (Watson 1940, p. 201; figs. 2—4), *Macrerpeton* (Romer 1930, p. 121; fig. 21), *Baphetes* (Watson 1929, p. 240; fig. 20), *Orthosauriscus* (Watson 1926, p. 210; figs. 6, 7), and *Leptophractus* (Romer 1930, p. 128; figs. 23, 24) from the Carboniferous; *Trimerorhachis* (v. Huene 1913, p. 372; fig. 56; Williston 1915, fig. 2), *Trematops* (Mehl 1926, pp. 470—471; fig. 3), *Zatrachys* (Broom 1913, fig. 21), *Eryops* (Case 1911, p. 92; figs. 25, 26; v. Huene 1913, p. 318; fig. 1; Broom 1913, p. 581; figs, 11, 19; Wegner 1922, fig. 31) from the Permian; and *Micropholis* (Watson 1913 a, p. 341; figs. 1, 2; Broili and Schröder 1937, p. 22; fig. 1; Wegner 1922, fig. 32), *Lydekkerina* (Watson 1913 a, p. 341; Broom 1915, p. 366; Watson 1919, fig. 9; Broili and Schröder 1937 a, fig. 1), *Trematosaurus* (H. Wagner 1935, fig. 10), *Trematosuchus*[1] (Haughton 1915, p. 48; pl. 8, fig. 2; Riabinin 1927; Kusmin 1935, p. 48; figs. 1, 3), *Thoosuchus* (Efremov 1940, fig. 6 C), *Platystega* (Säve-Söderbergh 1935, fig. 62; 1936, p. 48; figs. 18, 19), *Tertrema* (Säve-Söderbergh 1936, p. 114; fig. 50), and *Lyrocephalus* (Säve-Söderbergh 1935, pp. 37, 154, 166—167, 173; figs. 60, 61, 63, 64; 1936, p. 10; figs. 1, 2) from the Triassic. Of these forms *Eugyrinus* and *Miobatrachus* are placed by Watson (1940) in the order *Phyllospondyli*, which is closely akin to the order *Labyrinthodontia.* All the other forms enumerated belong to the order Labyrinthodontia, in which, following Romer (1939; cf. Steen 1938, p. 275), I shall here include also the *Phyllospondyli.* As far as I can find no septomaxillary has so far been observed in the *Adelospondyli*, *Lepospondyli* and *Anthracosauria.*

Judging from the incomplete descriptions of it in the literature the septomaxillary of Labyrinthodont Stegocephalians seems normally to be made up of two parts: a facial part situated at the postero-ventral or posterior corner of the fenestra exonarina anterior, and a medial process extending inwards into the nasal cavity. The facial part, which is best known, normally partakes in the formation of the skull-roof, and its outer face is ornamented in the same way as the adjacent dermal bones of the skull-roof. It is often connected by sutures posteriorly with the lachrymal and ventrally either with the maxillary or both with the maxillary and the "premaxillary", whereas its dorsal or anterior margin borders the fenestra exonarina anterior. Its position below or behind the fenestra exonarina anterior and its sutural connections thus favour the belief that it corresponds to the pars facialis of the lateral rostral in *Osteolepiformes* (*R. l*, figs. 34, 68 A, 86 A), though, compared with that, it is small. The medial process of the septomaxillary in Labyrinthodont Stegocephalians is insufficiently known. In certain forms, (e. g. *Trematops*; MEHL 1926, fig. 3), however, it is highly suggestive of the processus dermintermedius of the lateral rostral in *Osteolepiformes* (*pr. dim*, figs. 52 B, 53, 68 A, 70 A, 71 A; p. 449), and it thus seems reasonable to assume that it is homologous of that process. If this is true, the development of the nasal cavity and nasal sac in Labyrinthodont Stegocephalians was in one fundamental character as in *Osteolepiformes*. The processus dermintermedius is so special a formation that it can hardly be imagined to have arisen independently in *Osteolepiformes* and *Anura* on the one hand, and in Labyrinthodont Stegocephalians on the other.

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[1] Cf. foot-note 2 on p. 631.

In *Miobatrachus* WATSON (1940, p. 201; fig. 4) has recently described a ventral part of the septomaxillary which seems to correspond to the palatal process of the lateral rostral in *Osteolepiformes* (*R. l. pal*, figs. 52 B, 53, 58, 71 A, 86 A; p. 450). This ventral part of the septomaxillary in *Miobatrachus* is a small plate of bone situated on the ventral side of the ethmoidal region, wedged in between the hinder part of the "premaxillary" and the antero-lateral corner of the vomer and forming the anterior boundary of the fenestra exochoanalis. The palatal process of the lateral rostral in *Eusthenopteron* has quite the same position, but is covered ventrally by the postero-lateral part of the pars palatina (Pmx_3, NRP_3) of the (naso-rostro-)premaxillary and is therefore not exposed on the palatal side of the snout (cf. figs. 52 B, 56, 58).

According to WATSON (1940, p. 201) there issues from the ventral part of the septomaxillary in *Miobatrachus* "a small and short upstanding rod lying free and not in contact with other bones, but certainly visible through the external nostril". WATSON regards *Miobatrachus* as a form belonging to the direct ancestors of the Anurans and the upstanding rod in the nasal cavity would then have given rise to the septomaxillary in Anurans. It is not clear how the said rod could be modified into a septomaxillary of the peculiar horseshoe-shaped type (*Smx*, figs. 29, 69;

pp. 317—319) found in Anurans and gain relations to the recesses of the nasal cavity and the nasolachrymal duct corresponding to those of the septomaxillary in Anurans. Judging from WATSON's description and figures the septomaxillary in *Miobatrachus* has neither a pars facialis nor a medial process extending into the nasal cavity. This seems very strange since in most other Stegocephalians in which it is found preserved, inter alia in *Eugyrinus*, which according to WATSON is closely akin to *Miobatrachus*, the septomaxillary is provided with both the said formations.

As may be gathered from the above, the septomaxillary in Labyrinthodont Stegocephalians presents the following parts: 1) a facial part homologous to the pars facialis of the lateral rostral in *Osteolepiformes*; 2) a medial process projecting inwards into the nasal cavity and probably homologous to the processus dermintermedius of the lateral rostral in *Osteolepiformes*; and 3) at least in certain forms, e. g. *Miobatrachus*, also a palatal part corresponding to the palatal process of the lateral rostral in *Osteolepiformes*. The septomaxillary in Labyrinthodont Stegocephalians thus corresponds completely in position and structure to the lateral rostral in Osteolepiform Crossopterygians. The lateral rostral in *Porolepiformes* is of quite a different type, for it is devoid of a processus dermintermedius (pp. 369, 490—491). The lateral rostral in *Osteolepiformes* (chiefly the processus dermintermedius), has developed into the septomaxillary of Anurans (see pp. 529—535). The lateral rostral in Urodeles, on the other hand, has disappeared completely and the so-called septomaxillary in Urodeles (the nariodal bone) is a cartilage-bone in the lateral nasal wall and has nothing whatever to do with the lateral rostral or the septomaxillary (pp. 249, 293—295, 402, 414). In these circumstances it is obvious that the fundamental points of agreement between Labyrinthodont Stegocephalians and *Osteolepiformes* as regards the septomaxillary are of great importance and can only mean that the nasal cavity and nasal sac in Labyrinthodont Stegocephalians were developed essentially as in *Osteolepiformes* and Anurans and not as in *Porolepiformes* and Urodeles. This thus corroborates the opinion maintained above all by SÄVE-SÖDERBERGH (1936) and WATSON (1940) that Anurans and Labyrinthodont Stegocephalians are closely akin, whereas it decidedly contradicts the view advanced by BYSTROW (1939) and BYSTROW and EFREMOV (1940) that the Labyrinthodonts are most closely affined to the Urodeles.

In this connection it is of interest that the septomaxillary of reptiles and mammals (cf. FUCHS 1911; WEGNER 1922; STADTMÜLLER 1936 a, p. 928; DE BEER 1937, p. 442; T. E. WHITE 1939, p. 329) is also a dermal bone resembling the lateral rostral of *Osteolepiformes*.

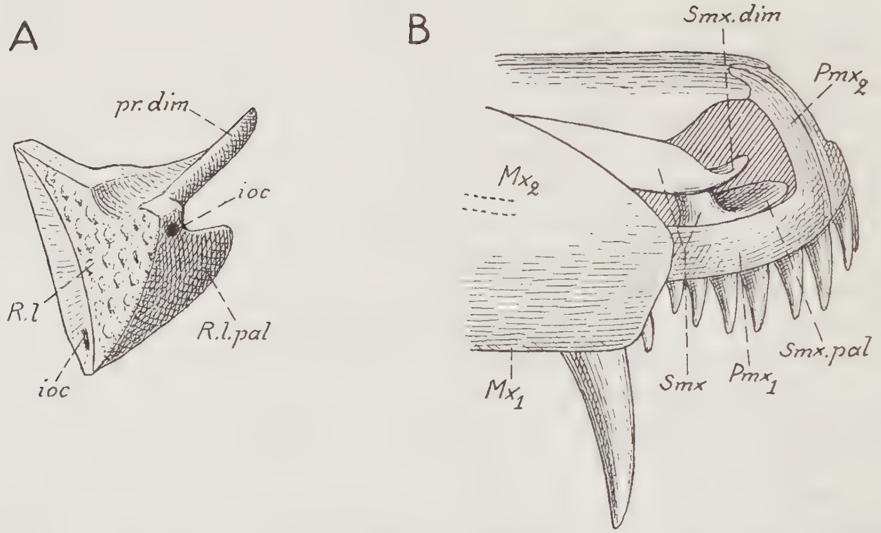

Fig. 86. *A, Eusthenopteron foordi* Whiteaves. Restoration of the right lateral rostral in antero-ventro-lateral view. $^{5}/_{1}$. *B, Scylacosaurus,* a Permian Therocephalian reptile. Anterior part of the skull in antero-lateral view, showing the septomaxillary in position in relation to the adjacent bones. After Watson, from Wegner (1922, fig. 39 A).

Mx_1, Mx_2, pars dentalis and pars facialis of maxillary; Pmx_1, Pmx_2, pars dentalis and pars facialis of "premaxillary" (naso-rostro-premaxillary?); *R. l,* lateral rostral (pars facialis); *R. l. pal,* processus palatinus of lateral rostral; *Smx,* pars facialis of septomaxillary (Pars facialis and Pedunculus of Wegner's description), corresponding to pars facialis of lateral rostral in *Eusthenopteron*; *Smx. dim,* process of septomaxillary extending into nasal cavity (Processus intrafenestralis, Wegner), homologous to processus dermintermedius of lateral rostral in *Eusthenopteron*; *Smx. pal,* processus palatinus of septomaxillary (Pars horizontalis, Wegner), homologous to processus palatinus of lateral rostral in *Eusthenopteron*; *ioc,* infraorbital sensory canal; *pr. dim,* processus dermintermedius of lateral rostral.

In primitive forms it is developed essentially as that bone of *Osteolepiformes,* to which it is beyond doubt strictly homologous. This is illustrated by fig. 86, which shows that the septomaxillary of the Permian Therocephalian *Scylacosaurus* (fig. 86 B), just as the lateral rostral in *Eusthenopteron* (fig. 86 A), consists of a facial part (*Smx,* fig. 86 A; Pars facialis and Pedunculus of Wegner's description) entering in the formation of the skull-roof, a medial process (*Smx. dim*; Processus intrafenestralis of Wegner's description) corresponding to the processus dermintermedius (*pr. dim,* fig. 86 A), and a palatal process (*Smx. pal*; Pars horizontalis of Wegner's description) overlapping the pars palatina of the "premaxillary". The presence of a septomaxillary of this type in reptiles and mammals indicates that these groups probably are descendants of *Osteolepiform*-like ancestors and thus, as maintained by Säve-Söderbergh (1934; 1935, p. 201), belong to the same large group (*Eutetrapoda*) as the *Labyrinthodontia* and *Anura,* but not to the same group as the *Urodela.*

In *Porolepis* the posterior external nasal tube, homologous to the nasolachrymal duct in Tetrapods[1] (see p. 402), pierces the fenestra exonarina posterior (*fe. exp*, fig. 41; cf. *fe. ex*, fig. 33), which is bounded anteriorly by the posterior border of the pars facialis of the lateral rostral and posteriorly by the anterior border of the lachrymal. Immediately outside this opening in *Porolepis*, and thus far in front of the orbital opening, was the posterior external nostril. During the development of the Urodeles from *Porolepiformes* the posterior external nasal tube must in connection with its modification into the nasolachrymal duct have grown backwards and become secondarily enclosed in the anterior part of the lachrymal (pp. 405—409). In no Urodele form does this duct pierce the entire lachrymal. On the other hand it does in the few Stegocephalians (*Micropholis*, WATSON 1913 a, pp. 341—342; fig. 2; *Branchiosaurus*, WATSON 1940, fig. 22; cf. also *Miobatrachus*, WATSON 1940, p. 199 and *Batrachosuchus*, WATSON 1919, p. 44) in which its course is known at present. If these Stegocephalians were descendants from *Porolepiformes*, they would be more advanced than Urodeles with regard to the relations between the nasolachrymal duct and the lachrymal. In *Osteolepiformes* the posterior external nasal tube was already developed as a nasolachrymal duct and passed backwards to the antero-lateral part of the orbit through the postnasal wall medially to both the lateral nasal wall and its dermal bones (pp. 446—447, 467). During the development of the Anurans from the *Osteolepiformes* the lateral part of the ethmoidal region was reduced, the nasolachrymal duct becoming situated immediately medially to the lachrymal, so that it may be imagined that it gradually gained a closer connection with the lachrymal and was completely enclosed in that bone. What is known so far concerning the position of the nasolachrymal duct in Stegocephalians thus favours the belief that the Stegocephalians are descendants from *Osteolepiformes* rather than from *Porolepiformes*.

The palate of *Osteolepiformes* has previously been compared to that of Stegocephalians (WATSON 1926; SÄVE-SÖDERBERGH 1932 a, p. 98; KUSMIN 1938; PARRINGTON and WESTOLL 1940) and it is already well known that as regards the number, position and general development of the dermal bones it is in several respects very much as in Stegocephalians. However, after the present investigations we are able to undertake a much more detailed comparison between the anterior part of the palate in *Osteolepiformes* and Stegocephalians. Also the anterior part of the palate can now to a certain extent be compared in *Porolepiformes* and Stegocephalians. In the preceding it has been shown that as regards the anterior part of the palate there are great similarities between *Porolepiformes* and *Urodela* (pp. 415, 419—421) on the one hand and *Osteolepiformes* and *Anura* (pp. 498—500) on the other. We shall here try to ascertain whether the various forms of Stegocephalians with regard to the structure of the anterior part of the palate are referable to the *Porolepiformes - Urodela* type or to the *Osteolepiformes - Anura* type.

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[1] The opinion maintained by SOLGER (1876), BORN (1883, p. 190), PIERSOL (1887, pp. 606—607) and WATSON (1913 a) that the nasolachrymal duct is a modified sensory canal cannot possibly be true (cf. FRANZ 1934, p. 1092).

The anterior part of the palate in *Osteolepiformes* (figs. 56, 64 A, 87 A) is characterized above all by the following features. In front of the vomers and underneath the divisio prenasalis communis there is a comparatively large transverse gap between the dermal bones, the anterior palatal fenestra (*fe. pal*), in which the lower face of the divisio prenasalis communis of the endocranium is exposed. This fenestra is not developed for any of the tusks of the lower jaws but was traversed by tubes of the paired intermaxillary gland, the prenasal nerve anastomoses (*ast. pren*, fig. 60) and vessels. It lies in the roof of a special fossa, the fossa apicalis (*fo. ap*), in the foremost part of the palate. In the roof of this fossa, partly in the lower face of the divisio prenasalis communis and partly in the lower face of the vomer, there is a paired pit, the prenasal pit (*fo. pren*), which housed the main parts of the intermaxillary gland. The fossa apicalis is bounded posteriorly chiefly by the antero-medial transverse parts of the descending tooth-bearing laminae of the vomers (*la. Vo*). In the ventral face of the anterior medial parts of the vomers and in the adjacent medial parts of the anterior face of the descending tooth-bearing laminae is a median unpaired pit, the intervomerine pit (*fo. iv*), which continues backwards by a median canal, the intervomerine canal (*c. iv*), or opens backwards through an opening between the descending tooth-bearing laminae of both sides (cf. p. 487). This canal or opening housed the efferent duct of the intermaxillary gland, which went backwards and opened in the roof of the mouth behind the fossa apicalis and close underneath the anterior end of the parasphenoid. Each vomer is produced backwards along the parasphenoid into a long posterior process (*pr_p Vo*). The parasphenoid (*Psph*) is narrow and extends forwards approximately to the posterior wall of the fossa apicalis. On its ventral face, though not most anteriorly, the parasphenoid has a median tooth-bearing ridge (*ri. Psph*). The entopterygoids (*Enpt*) do not meet in a median suture, being separated by the lowermost part of the interorbital wall. Between the entopterygoid of either side and the interorbital part of the parasphenoid is a narrow space, the interpterygoid fenestra (*fe. ipt*, figs. 55, 56). The anterior part of the palate in Anurans is essentially as in *Osteolepiformes* with the difference that the skeleton is much reduced (pp. 496—500).

An anterior palatal fenestra is developed also in *Porolepiformes* (figs. 36 A, 37 A, 39, 44; p. 415), but contrary to conditions in the *Osteolepiformes* it lies mainly underneath the internasal wall between the vomers, the anterior parts of which are consequently wide apart. This fenestra in *Porolepiformes* is the common ventral opening of the paired cavum internasale (*cav. in*), which probably lodged the paired intermaxillary gland (cf. pp. 400—401). The vomer has no descending tooth-bearing lamina and no posterior process and consequently the *Porolepiformes* have no fossa apicalis, intervomerine pit or intervomerine canal. The parasphenoid is broad and extends but slightly forwards underneath the ethmoidal region. The anterior part of the palate is in primitive Urodeles (*Onychodactylus*) essentially as in *Porolepiformes* (p. 415). The *Porolepiformes* agree with the *Osteolepiformes* as regards the medial extent of the entopterygoids, which do not meet in a median suture and are separated from the interorbital part of the parasphenoid by narrow interpterygoid fenestrae.

In Ichthyostegids we find in the foremost part of the palate in front of the vomers a transverse fenestra (Säve-Söderbergh 1932 a, *apv*, figs. 5, 8, 9), which both in position and shape agrees well with the anterior palatal fenestra in *Osteolepiformes* and may be presumed to be homologous to that. The presence of this fenestra renders it very likely that Ichthyostegids had an intermaxillary gland situated essentially as in *Osteolepiformes* and Anurans (cf. Säve-Söderbergh 1935, pp. 26—28 and below p. 634).

The entopterygoids in Ichthyostegids (Säve-Söderbergh 1932 a, figs. 5, 8, 9, 13) are more strongly developed than in *Osteolepiformes* (fig. 87 A). They extend forwards between the posterior parts of the vomers and have a fairly long contact with each other in the median line. The vomer seems to lack a posterior process along the parasphenoid corresponding to the posterior process of the vomer (*pr$_p$ Vo*) in *Osteolepiformes* and primitive Anurans (*Ascaphus*, p. 499; cf. fig. 64 B). The anterior part of the parasphenoid in Ichthyostegids (Säve-Söderbergh 1932 a, figs. 5, 9, 13; pls. 4, 15; pl. 17, fig. 2; cf. pl. 8) is narrow, but owing to the strong development of the entopterygoids this bone does not, as far as known, extend so far forwards as it does in *Osteolepiformes* and Anurans (cf. p. 500). The Ichthyostegids thus differ in several respects from the *Osteolepiformes* in the structure of the palate. If the Ichthyostegids are derived from Osteolepiform ancestors, their entopterygoids must have undergone a progressive development. Through the excessive development of the entopterygoids, the posterior processes of the vomers and the anterior part of the parasphenoid lost their importance and disappeared. The anterior parts of the palate in the Ichthyostegids are thus in fact more specialized than in most Postdevonian Stegocephalians (fig. 87 B; p. 637) and primitive Anurans (cf. fig. 64), in which the Osteolepiform type of palate is retained in a less modified condition. Not only the ventral position of the external nostril and the absence of the lateral rostral, but also the development of the anterior part of the palate thus indicate that the Ichthyostegids cannot be transitional between *Osteolepiformes* and *Anura.* It is also obvious that they cannot be intermediate between *Porolepiformes* and *Urodela.* The presence of an anterior palatal fenestra of Osteolepiform type indicates, however, that they are probably an early offshoot from the Osteolepiform—Anuran stock. On other grounds they were regarded already by SÄVE-SÖDERBERGH (1932 a, pp. 102—105; cf. WESTOLL 1942, p. 121) as an early side branch of the stem of Labyrinthodont Stegocephalians.

A palate in which the entopterygoid meets its fellow in the median line in the same way as in Ichthyostegids is also met with in Loxommoids among the *Labyrinthodontia* (*Orthosauriscus*, WATSON 1926, fig. 9; *Baphetes*, WATSON 1926, fig. 4 A; 1929, fig. 19; *Macrerpeton*, ROMER 1930, fig. 21), in *Batrachiderpeton* (WATSON 1913) among the *Lepospondyli* and in the *Anthracosauria* (*Pholiderpeton*, *Anthracosaurus*, *Pholidogaster*, WATSON 1929, figs. 2, 3, 11). Like the Ichthyostegids these forms are probably neither transitional between *Porolepiformes* and *Urodela* nor between *Osteolepiformes* and *Anura.* The presence of a true septomaxillary and an anterior palatal fenestra of Osteolepiform type (in *Orthosauriscus*; see below) indicates that at least the Loxommoids belong (as a specialized offshoot) to the line of evolution leading from *Osteolepiformes* to *Anura.*

According to the figures and descriptions published no anterior palatal fenestra exists in Loxommoids, except in *Orthosauriscus* (see below), nor in the majority of other Palaeozoic *Labyrinthodontia* (*Amphibamus*, *Miobatrachus*, *Eugyrinus*, WATSON 1940, figs. 1, 4, 13; *Erpetosaurus*, *Stegops*, ROMER 1930, figs. 16, 18; STEEN 1930, figs. 5, 10; *Branchiosaurus*, *Leptorophus*, *Micromelerpeton*, BULMAN and WHITTARD 1926, figs. 1, 5, 9, 11; *Platyrhinops*, STEEN 1930, fig. 13, among the "*Phyllospondyli*", *Nyrania*, *Cochleosaurus*, *Potamochoston*, STEEN 1938, figs. 28, 30, 37; *Dendrerpeton*, STEEN 1934, fig. 4; *Sclerocephalus*, BROILI 1926; *Eryops*, BROOM 1913, fig. 12; *Rhinesuchus*, WATSON 1919, fig. 3; *Archegosaurus*, WATSON 1919, fig. 2; HOFKER 1927; WHITTARD 1928, among the "*Rhachitomi*"). The same applies to the Triassic Rhachitomous forms *Micropholis* (WATSON 1913 a; BROILI and SCHRÖDER 1937) and *Sclerothorax* (v. HUENE 1932) and to the Mesozoic Brachyopids and Plagiosaurids among the Stereospondylous Labyrinthodonts (*Batrachosuchus*, WATSON 1919, fig. 27; *Plagiosternum*, *Plagiosuchus*, v. HUENE 1922, figs. 14, 27; *Gerrothorax*, v. HUENE 1922, fig. 31; NILSSON 1937, fig. 14; cf. pp. 52, 53 and NILSson 1939, pp. 3, 9), and, as far as I can find, also to the exclusively Palaeozoic *Anthracosauria* (*Pholiderpeton*, *Anthracosaurus*, *Pholidogaster*, Watson 1929, figs. 2, 3, 11), *Adelospondyli* (*Microbrachis*, *Hyloplesion*, Steen 1938, figs. 15 and 21; "*Hylonomus*", Watson 1940, fig. 11; cf. Steen 1938, p. 272) and *Lepospondyli* (*Scincosaurus*, *Ricnodon*, Steen 1938, figs. 7, 14; *Diplocaulus*, Douthitt 1917; *Batrachiderpeton*, Watson 1913; *Diceratosaurus*, Jaekel 1903, pl. 3). It is of interest that these forms also include *Miobatrachus*, which is regarded by Watson (1940, p. 229) as the ancestral form of the *Anura*. The absence of the anterior palatal fenestra, and other conditions, show that all the forms here enumerated are obviously too highly specialized to have given rise to either Urodeles or Anurans. At any rate they cannot possibly be transitional between *Porolepiformes* and *Urodela* or between *Osteolepiformes* and *Anura*.

A palatal opening situated as the anterior palatal fenestra in *Osteolepiformes* and Ichthyostegids is encountered in numerous *Labyrinthodontia*, e.g. in *Orthosauriscus* (Watson 1926, fig. 9) among the Loxommoids and *Pelion*[1] (Romer 1930, fig. 6), also from the Carboniferous, in certain Permian forms (e.g. *Acanthostoma*, Steen 1937; *Dasyceps*, v. Huene 1910; *Trematops*, Olson 1941, fig. 8; cf. Mehl 1926, fig. 4; *Trimerorhachis*, Case 1935; *Melosaurus*, Efremov 1937; Hartmann-Weinberg 1939; and *Dvinosaurus*, Bystrow 1938), in the Triassic Rhachitomous form *Lydekkerina* (Watson 1919, fig. 6; Broili and Schröder 1937 a), and in the majority of the Triassic Stereospondylous Labyrinthodonts (Capitosauroids, e.g. *Capitosaurus*, Watson 1919, fig. 29 C; Roepke 1923; Edinger 1937; Broili and Schröder 1937 b; *Cyclotosaurus*, Fraas 1889; 1913; v. Huene 1920, fig. 12; *Wetlugasaurus*, Riabinin 1930, fig. 2; pl. 6; Kusmin 1938, pl. 1; *Kestrosaurus*, Haughton 1925, fig. 12; *Benthosuchus*, Bystrow 1935; Bystrow and Efremov 1940; *Thoosuchus*, Efremov 1940, fig. 2; *Sassenisaurus*, Nilsson 1942; *Heptasaurus*, fig. 87 B; Wepfer 1923; Pfannenstiel 1932, fig. 5; pl. 1, fig. A; *Mastodonsaurus*, Fraas 1889; v. Huene 1920, fig. 10; Metoposaurids, as *Metoposaurus*, Watson 1919, fig. 20; Bystrow 1935, fig. 34 A; *Anaschisma*, *Koskinonodon*, *Borborophagus*, Branson and Mehl 1929, figs. 6, 7, 8, 10; *Buettneria*, Branson and Mehl 1929, fig. 3; Case 1931; 1932 and Trematosaurids, e.g. *Trematosaurus*, Burmeister 1849; Watson 1919, fig. 25; Drevermann 1920; v. Huene 1921; H. Wagner 1935; *Trematosuchus*[2], Haughton 1925, fig. 15; Riabinin 1927; Kusmin 1935; *Microposaurus*, Haughton 1925, fig. 18; *Lyrocephalus*, *Platystega*, *Tertrema*,

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[1] According to Romer (1939, p. 759) *Pelion* may be a larva of *Leptophractus lancifer* or a similar type.

[2] According to Efremov (1940, p. 93; 1940 a, p. 381) *Trematosuchus weidenbaumi* Kusmin and (?) *Trematosuchus yakovlevi* Riabinin belong to the genus *Thoosuchus*.

Säve-Söderbergh 1936, figs. 4, 5, 20, 21, 51). The palatal fenestra in these forms may be paired (*Pelion*, *Trimerorhachis*, *Melosaurus*, *Dvinosaurus*, *Kestrosaurus*, old specimens of *Benthosuchus*, *Heptasaurus*, *Thoosuchus*, *Mastodonsaurus*, *Metoposaurus*, *Anaschisma*, *Koskinonodon*, *Borborophagus*, *Buettneria*, *Trematosaurus*, *Trematosuchus*, *Microposaurus*, *Lyrocephalus*, *Platystega*, *Tertrema*), or unpaired (*Orthosauriscus*, *Acanthostoma*, *Dasyceps*, *Trematops*, *Lydekkerina*, *Capitosaurus*, *Cyclotosaurus*, *Wetlugasaurus*, *Benthosuchus*, *Sassenisaurus*) as in *Osteolepiformes* and Ichthyostegids, and varies somewhat in shape and extent. In order to illustrate the similarities in the development of this opening and the anterior parts of the palate otherwise these Stegocephalians will now be compared with *Eusthenopteron*.

Fig. 87 shows the anterior parts of the palate in *Eusthenopteron foordi* and *Heptasaurus* (*Mastodonsaurus cappelensis* Wepfer; cf. Säve-Söderbergh 1935, p. 79; Nilsson 1942, p. 95, foot-note 1) in ventral aspect. The dermal bones of the palate in these two forms are present in the same number and are so alike in all main features that it cannot be doubted that the correspondingly termed bones actually are homologous formations. The maxillary (*Mx*) in *Heptasaurus* differs, however, from that in *Eusthenopteron* since it is provided with a palatal process (Mx_3) and extends further forwards. Correlative with this forward extent of the maxillary the naso-rostro-premaxillary is shorter in *Heptasaurus* than in *Eusthenopteron* (cf. p. 497). Finally, in *Heptasaurus* the entopterygoid (*Enpt*) is much more weakly developed and far narrower, and consequently the interpterygoid fenestra (*fe. ipt*) is considerably larger than in *Eusthenopteron*. *Heptasaurus* thus differs from *Eusthenopteron* as regards the structure of the anterior part of the palate in the same way as do the *Anura*, and must therefore have undergone a similar phyletic development in this respect as the *Anura*. Apart from the differences now referred to, which obviously are secondary, the agreement between *Heptasaurus* and *Eusthenopteron* is very striking and includes many details. The vomer (*Vo*, fig. 87) in the two forms is of a corresponding triangular shape, produced backwards in a posterior process ($pr_p\,Vo$) along the parasphenoid and provided with a descending tooth-bearing lamina (*la. Vo*) consisting of an anterior transverse portion and a posterior longitudinal portion situated just medially to the fenestra exochoanalis (*fe. exch*). The anterior transverse portions of the descending tooth-bearing laminae of the vomers meet in a median suture and form together the posterior wall of the fossa apicalis (*fo. ap*). On the anterior side of this wall, i. e. in the hinder part of the fossa apicalis, there is in both forms a median unpaired intervomerine pit (*fo. iv*). Immediately behind the median suture between the two vomers there is in *Heptasaurus*

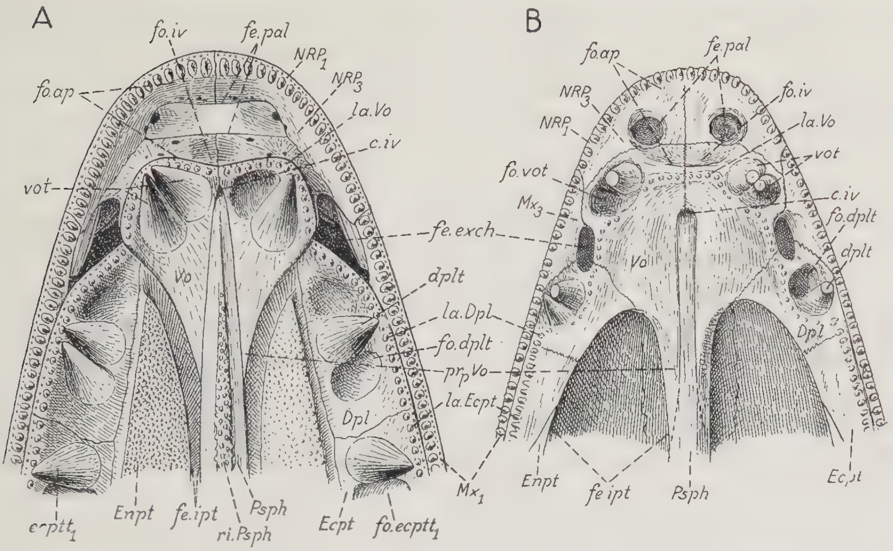

Fig. 87. Anterior parts of the palate in ventral view. *A*, *Eusthenopteron foordi* Whiteaves. $^9/_5$. *B*, *Heptasaurus* ("*Mastodonsaurus*") *cappelensis* (Wepfer), a Triassic Labyrinthodont Stegocephalian. Compilation from Wepfer (1923, figs. 6 and 11). $^1/_5$.

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; Mx_1, Mx_3, pars dentalis and pars palatina of the maxillary; NRP_1, NRP_3, pars dentalis and pars palatina of the naso-rostro-premaxillary; *Psph*, parasphenoid; *Vo*, vomer; *c. iv*, intervomerine canal; *dplt*, dermopalatine tusks; $ecptt_1$, tusk of the anterior pair of the ectopterygoid tusks; *fe. ipt*, interpterygoid fenestra; *fe. pal*, anterior palatal fenestra; *fe. exch*, fenestra exochoanalis; *fo. ap*, fossa apicalis; *fo. dplt*, *fo.* $ecptt_1$, pits after missing dermopalatine and ectopterygoid tusks; *fo. iv*, intervomerine pit; *fo. vot*, fossa after missing vomerine tusk; *la. Dpl*, *la. Ecpt*, *la. Vo*, vertical tooth-bearing laminae of dermopalatine, ectopterygoid and vomer; $pr_p Vo$, posterior process of vomer; *ri. Psph*, ventral tooth-bearing ridge of parasphenoid; *vot*, vomerine tusk.

a distinct pit (*c. iv*) at the very anterior tip of the parasphenoid. This pit lies in approximately the same place as the posterior orifice of the intervomerine canal (*c. iv*, pp. 459—461) in *Eusthenopteron*. Though this is not described by Wepfer (1923), it is evident that an intervomerine canal must exist also in *Heptasaurus*, the pit just referred to being its posterior orifice (cf. *Mastodonsaurus acuminatus*, Fraas 1889, pl. 7). In *Heptasaurus*, as in *Eusthenopteron*, the foremost parts of the vomers, situated in front of the descending tooth-bearing laminae, and the palatal processes (NRP_3) of the naso-rostro-premaxillaries enter in the formation of the roof of the fossa apicalis. Unlike that of *Eusthenopteron* the anterior palatal fenestra in *Heptasaurus* (*fe. pal*) is paired. This difference is not, however, of a profund nature, for in *Eusthenopteron* the fenestra also shows a slight tendency to a subdivision into right and left halves and is unpaired and developed very much as in *Eustenopteron* in such Stegocephalians as *Capitosaurus*, *Cyclotosaurus*, *Wetlugasaurus* and

Benthosuchus (cf. above), all of which are akin to *Heptasaurus*. It is also interesting that each palatal fenestra in *Heptasaurus* has a corresponding position as the main anterior part of the prenasal pit in *Eusthenopteron* (*fo. pren*, fig. 56), which must have housed the main portion of the paired intermaxillary gland (p. 506). This, and the presence of the intervomerine pit and canal, must obviously mean that *Heptasaurus* had an intermaxillary gland with a position and development fundamentally as in *Eusthenopteron*. The position of the main portion of the intermaxillary gland in *Eusthenopteron* in a pit (the anterior half of the prenasal pit) in the lower face of the divisio prenasalis communis of the ethmoidal region, the fact that the ethmoidal region of the neural endocranium in Stegocephalians as far as known was unossified, and the presence of an interrostral fenestra[1] in the anterior part of the dermal cranial roof in certain forms (e. g. *Zatrachys*, *Dasyceps*, *Acanthostoma*, *Trematops*, *Micropholis* and *Miobatrachus*; see SÄVE-SÖDERBERGH 1935, pp. 23—28; WATSON 1940, fig. 2) render it highly probable that the intermaxillary gland in Stegocephalians was more strongly developed than in *Eusthenopteron* and was situated mainly dorsally to the anterior palatal fenestra in a space corresponding to the cavum prenasale of Anurans (cf. SÄVE-SÖDERBERGH 1936, figs. 7, 8; BYSTROW and EFREMOV 1940, figs. 32, 33). In the roof of the anterior part of the prenasal pit in *Eusthenopteron*, which is a cavum prenasale of Anuran type in an initial stage of development (p. 502), lies the ventral opening of the wide ventral branch (*c_vn-b*, figs. 56, 57) of the nasobasal canal (*c. n-b*, see p. 470). This ventral branch presumably gave passage 1) to the ventral terminal branch (*$r_v$mn*, figs. 60, 61) of the r. medialis narium of the n. profundus, which in the prenasal pit probably passed over into the medial terminal branch (*$r_m$pal*) of the r. palatinus and formed the prenasal nerve anastomosis (*ast. pren*); 2) to a prenasal arterial anastomosis; and 3) probably also to tubes of the intermaxillary gland which through the nasobasal canal entered the nasal cavity (p. 506). Very likely prenasal nerve and arterial anastomoses were present also in *Heptasaurus* and allied forms. Both in *Eusthenopteron* and *Heptasaurus* the vomer is provided with one or two large tusks (*vot*, fig. 87), one of which is generally missing. In *Heptasaurus*, however, these tusks are situated just antero-laterally (externally) to the anterior part of the descending tooth-bearing lamina, whereas in *Eusthenopteron* they are developed postero-medially (internally) to the corresponding lamina. Both in *Heptasaurus* and *Eusthenopteron* the vomer is in sutural connection antero-laterally with the pars palatina

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[1] The opinion recently advanced by OLSON (1941, p. 162) that the interrostral fenestra in *Trematops* is a "median narial opening" which to all appearances "functioned as accessory breathing apparatus" cannot possibly be true.

(NRP_3) of the naso-rostro-premaxillary. In *Heptasaurus* it also has a sutural connection postero-laterally with the dermopalatine. No corresponding suture is found in *Eusthenopteron*, but the vomer and dermopalatine are intimately and rigidly connected and the dermopalatine overlaps the dorsal face of the vomer (p. 456), as it does at least in certain Stegocephalians akin to *Heptasaurus* (*Benthosuchus*, BYSTROW and EFREMOV 1940, p. 123; fig. 2; *Sassenisaurus*, NILSSON 1942, fig. 1). The dermopalatine (*Dpl*) in both has a descending tooth-bearing lamina (*la. Dpl*) in the posterior prolongation of the rostro-caudal portion of the descending tooth-bearing lamina of the vomer. Besides it is provided with one or two large tusks. However, in *Heptasaurus* these tusks lie laterally (externally) to the tooth-bearing lamina, as do the vomerine tusks, whereas in *Eusthenopteron* they are developed medially (internally) to that lamina. Both in *Heptasaurus* and *Eusthenopteron* the parasphenoid (*Psph*) is narrow and extends approximately to the posterior wall of the fossa apicalis (cf. *Benthosuchus*, BYSTROW and EFREMOV 1940, figs. 8, 17, 21). In certain forms akin to *Heptasaurus* (*Cyclotosaurus posthumus*, FRAAS 1913, p. 290; *Benthosuchus*, BYSTROW and EFREMOV 1940, fig. 8) it has, as in *Eusthenopteron* (*ri. Psph*), a ventral ridge, which, however, bears no teeth.

The anterior parts of the palate in *Heptasaurus* are thus almost exactly as in *Eusthenopteron*. The agreement between these two forms in this respect is in fact so amazingly close that *Heptasaurus* must beyond doubt be regarded as a direct descendant from primitive *Osteolepiformes*.

The other Capitosauroids and the Metoposaurids are essentially as *Heptasaurus* as regards the anterior parts of the palate, and in this respect they thus also agree very well with *Eusthenopteron*. Also in these forms there is as a rule a well-defined fossa apicalis. In certain forms, such as *Benthosuchus* (BYSTROW and EFREMOV 1940), *Thoosuchus* (EFREMOV 1940), *Sassenisaurus* (NILSSON 1942), *Rhinesuchus* (YAKOVLEV 1918) and *Rasaurus*[1] (KUSMIN 1938, pl. 3, fig. 1), the anterior parts of the descending tooth-bearing laminae (or of the rows of teeth) of the vomers are not transverse, but meet in the median line at a V-shaped angle. As pointed out by KUSMIN (1938, p. 34) the descending tooth-bearing laminae of the vomers in certain specimens of *Eusthenopteron* (fig. 87 A) tend to meet in a corresponding way. The intervomerine pit and intervomerine canal are quite distinct in a skull of *Mastodonsaurus* figured by FRAAS (1889, pl. 7). That an intervomerine canal exists also in

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[1] *Rhinesuchus wolgodwinensis* Yakovlev and *Rasaurus* Kusmin probably belong to *Benthosuchus* or *Thoosuchus* (cf. EFREMOV 1940 a, p. 382; NILSSON 1942, p. 96, footnote 4).

Metoposaurids is obvious from the following quotation from CASE (1931, p. 191) concerning *Buettneria*: "The cultriform process of the parasphenoid is broad and extends as far forward as the transverse row of vomerine teeth, where it rises with the appearance of an opening between it and the vomerine teeth below" (cf. CASE 1932, p. 22; 1935, p. 250). The Trematosaurids differ from *Eusthenopteron* in being devoid of both the fossa apicalis and the intervomerine canal, but otherwise they agree in essentials with that form as regards the structure of the anterior part of the palate. The absence of the fossa apicalis and intervomerine canal in the Trematosaurids may be due to the fact that the descending tooth-bearing laminae of the vomers are highly reduced. Finally, in *Lydekkerina* the anterior part of the palate is also of essentially the same type as in *Heptasaurus* and *Osteolepiformes* (cf. NILSSON 1942, p. 96, foot-note 3).

The Stegocephalians now dealt with, which as regards the anterior part of the palate show so close and fundamental points of agreement with *Osteolepiformes*, viz. Capitosauroids, Metoposaurids, Trematosaurids and *Lydekkerina*, are all Triassic forms. On the other hand, the Permian Stegocephalians, which have an anterior palatal fenestra (p. 631), differ in the anterior part of the palate pretty considerably from *Osteolepiformes*, more, indeed, than the Triassic ones just enumerated. As far as I can see, these Permian forms are all developed in such a way that they cannot be regarded as transitional between *Osteolepiformes* and the Triassic Stegocephalians mentioned above. In *Dvinosaurus* and *Trimerorhachis* the vomer is provided with a postero-lateral process wedged in between the entopterygoid and the dermopalatine. There is no equivalent to this process either in *Eusthenopteron* or in the Triassic Stegocephalians here in question. On the other hand, the vomer both in *Dvinosaurus* and *Trimerorhachis* seems to be devoid of the posterior process ($pr_p Vo$) so characteristic of *Eusthenopteron* and the majority of Triassic Stegocephalians. Also *Trematops* seems to lack a posterior process of the vomer. The structure of the fenestra exonarina anterior and the presence of strong descending laminae of the nasals (OLSON 1941, p. 161; fig. 8 D) show that this form is highly specialized. Among forms with an anterior palatal fenestra *Melosaurus* seems to be the Permian Stegocephalian most closely approaching the *Osteolepiformes* and the Triassic Stegocephalians[1]. Among the Carboniferous Stegocephalians possessing an anterior palatal fenestra (see p. 631) *Orthosauriscus* differs strongly from *Osteolepiformes* as regards the development of the entopterygoids, vomers and parasphenoid (cf. p. 630). *Pelion* has retained certain Osteolepiform features, viz. the posterior process of the vomer and the ventral ridge of the parasphenoid, but in other respects, e. g. in the position of the teeth and in the absence of a descending lamina of the vomer, a fossa apicalis, an intervomerine pit and an intervomerine canal, it differs considerably from *Osteolepiformes* and the Triassic Stegocephalians with an anterior palatal fenestra.

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[1] According to HARTMANN-WEINBERG (1939, pp. 29—30) *Melosaurus* is closely related to *Archegosaurus*. It differs, however, from that form inter alia in the following respects: It possesses an anterior palatal fenestra; the fenestra exochoanalis is comparatively close to that of the opposite side; it has a posterior process of the vomer; and it possesses no postero-lateral process of the vomer.

Summing up what has now been set forth, we find that as regards the structure of the anterior parts of the palate it is the Triassic "*Stereospondyli*" exclusive of Brachyopids and Plagiosaurids that show the greatest agreement with *Osteolepiformes*. It is plainly seen that the anterior palatal fenestra in these Stegocephalians is a true homologue of that in *Osteolepiformes*. It is also fully evident that the intermaxillary gland in these Stegocephalians was in all essentials of an Osteolepiform —Anuran type. It appears to me rather difficult to assume that these Stegocephalians should have arisen from any Palaeozoic forms in which these parts of the palate were particularly modified or specialized. Consequently their ancestors can hardly be sought for in such Palaeozoic forms where the anterior palatal fenestra is absent, where the vomer is considerably modified and not of the Osteolepiform type, where the descending tooth-bearing laminae of the vomer and dermopalatine are much reduced or absent or where the entopterygoids meet in the median line underneath the interorbital wall and have caused a partial reduction of the parasphenoid and vomers.

That the majority of the Triassic "*Stereospondyli*" are very closely akin to *Osteolepiformes* and *Anura* is also evident from the course of the r. palatinus VII. In *Lyrocephalus* (Säve-Söderbergh 1936, pp. 16, 122; figs. 4, 52) this nerve gave off a lateral branch which together with a branch of the r. maxillaris V formed a postchoanal anastomosis corresponding to that in *Eusthenopteron* (*ast.pch*, figs. 60, 61) and *Rana* (fig. 31) and then entered the vomer from the dorsal side[1]. Also the forebrain in Triassic Stegocephalians (Säve-Söderbergh 1936, figs. 52, 53; Bystrow and Efremov 1940, fig. 37) was undoubtedly of the Osteolepiform—Anuran type. The bulbi olfactorii were thus situated close to one another in front of the hemispheres and not ventro-laterally to them and far apart as in *Porolepiformes* and *Urodela* (cf. pp. 395, 540; figs. 19 B, 30, 43, 59).

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[1] Figure 38 in Bystrow and Efremov (1940) shows the nerve in question in *Benthosuchus* breaking up terminally into two branches, anterior and lateral, and thus developed in the same way as in *Osteolepiformes* (figs. 60, 61) and *Anura* (fig. 31), but not as in Urodeles (figs. 20, 21). The figure by Bystrow and Efremov just referred to, which seems to have been meant to illustrate an agreement with Urodeles (Bystrow and Efremov loc. cit., p. 129; cf. Bystrow 1939), decidedly shows, instead, a course of the palatine nerve distinctive of Anurans. Another figure given by Bystrow and Efremov (1940, fig. 37) shows the n. profundus in *Benthosuchus* with, at least partly, a course corresponding to that in *Osteolepiformes* (figs. 58, 60) and *Anura* (figs. 29, 30). If correct, the nervous system of *Benthosuchus* as restored by Bystrow and Efremov

What has now been said thus corroborates the conclusion arrived at by Säve-Söderbergh (1936) that *Labyrinthodontia* and *Anura* are closely related groups. Säve-Söderbergh's conclusion was based on a thorough investigation of the skull of Trematosaurids and detailed comparisons with Anurans. He established that there is considerable agreement between Labyrinthodonts and Anurans as regards both the ethmoidal region and the anterior part of the palatoquadrate.

According to the current opinion the anterior palatal fenestra in Stegocephalians is developed for the tusks of the lower jaw. This is certainly true in some forms, such as *Mastodonsaurus* (Fraas 1889, pl. 1) and *Heptasaurus* (Wepfer 1923), where the tusks of the lower jaw pierce not only the palate but also the skull-roof. From what is now known concerning the palate in *Osteolepiformes*, Stegocephalians and *Anura* it is obvious, however, that this function of the anterior palatal fenestra must be a secondary one (cf. Jarvik 1937, p. 118) correlative with modifications in the dentition of Stegocephalians, which I shall not discuss in detail in this work[1]. It may be pointed out, however, that an anterior palatal fenestra is present in certain Stegocephalians (e. g. *Trematops*, Olson 1941, figs. 8, 10) which have no corresponding large tusks in the lower jaw, whereas, as far as known, it is absent in other forms (*Eryops*) in which the lower jaw is equipped with enlarged symphysial tusks (Broom 1913, figs. 12, 18).

The comparisons now made demonstrate that the structure of the anterior part of the palate in *Ichthyostegalia* and *Labyrinthodontia* is fundamentally as in *Osteolepiformes*. The anterior palatal fenestra, where persisting among representatives of these two groups of Stegocephalians, is clearly of the Osteolepiform type. Also the parasphenoid in these two groups is normally of a type corresponding to that in *Osteolepiformes*. A broad

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would rather seem to indicate that this form is closely akin to *Osteolepiformes* and *Anura*, but not to Urodeles as they seem to believe. However, as far as can be judged the restorations in the parts discussed are not supported by any evidence in the specimens.

[1] These modifications mainly consist of a reduction of the coronoid tusks, which in *Osteolepiformes* are strongly developed and opposed to the tusks of the vomer, dermopalatine and ectopterygoid. Correlative with this reduction of the coronoid tusks certain of the teeth of the dentary became transformed into tusks opposing those of the vomer, dermopalatine and ectopterygoid in the upper jaw.

parasphenoid similar to that in *Porolepiformes* and *Urodela* is found in Stegocephalians in a few forms only, e. g. in certain *Labyrinthodontia* (*Sclerothorax*, v. HUENE 1932, *Phrynosuchus*, HAUGHTON 1925, fig. 19, *Tungussogyrinus* EFREMOV 1939; cf. BYSTROW 1939, fig. 8) and *Adelospondyli* (*Lysorophus*, BROILI 1908; CASE 1908; BROOM 1918; SOLLAS 1920, *Cocytinus*, STEEN 1938, p. 272). Among these forms *Lysorophus* is of interest since it is regarded as a Urodele by several writers (ABEL 1919, pp. 326—329; HERRE 1935, p. 46). Whether any of these forms with a broad parasphenoid are in any way affined to *Porolepiformes* and *Urodela* cannot be ascertained by reference to the structure of the snout.

The main results gained from the above account of the snout in Stegocephalians may be summarized as follows.

1) The external nostril in Ichthyostegids was an anterior external nostril homologous to the anterior external nostril in Crossopterygians and Tetrapods. Its ventral position must be secondary and due to a downward migration from a primarily lateral position, and by this process the lateral rostral (septomaxillary) was pushed inwards into the lateral part of the roof of the mouth and probably became completely reduced.

2) The septomaxillary in *Labyrinthodontia* (including *Phyllospondyli*) is developed very much as the lateral rostral in *Osteolepiformes* and is beyond question strictly homologous to that bone. The same applies to the septomaxillary in primitive reptiles. The septomaxillary has not been observed in other Stegocephalians than the *Labyrinthodontia* (including *Phyllospondyli*).

3) As regards the structure of the anterior parts of the palate the Triassic Stegocephalians belonging to the families *Capitosauridae*, *Mastodonsauridae*, *Benthosuchidae*, and *Metoposauridae* are highly suggestive of Osteolepiform Crossopterygians. Though somewhat more specialized than the Stegocephalians mentioned the *Trematosauridae* also agree well with the *Osteolepiformes* in the respect here in question. The dermal bones of the palate are clearly homologous and developed in essentially the same way in all the Triassic Stegocephalians mentioned and in the *Osteolepiformes*. Quite as in *Osteolepiformes* there is also in these Stegocephalians an anterior palatal fenestra, and normally also a fossa apicalis, an intervomerine pit, and an intervomerine canal.

4) An anterior palatal fenestra homologous to that in *Osteolepiformes* is found in the Triassic forms mentioned and in the Ichthyostegids, but otherwise only in comparatively few Palaeozoic Labyrinthodonts.

5) The intermaxillary gland in at least several of the Labyrinthodonts was as regards position, shape, and efferent duct very much as in *Osteolepiformes*.

6) The anterior palatal fenestra in Stegocephalians was primarily developed for the intermaxillary gland and for certain nerves and vessels, but was subsequently modified in several forms so as to receive the large anterior tusks of the lower jaws.

7) It is not likely that Stegocephalians with a persistant anterior palatal fenestra have arisen from forms without such a fenestra.

8) Stegocephalians in which the parasphenoid is well developed in the ethmoidal part and in which the vomer is provided with a posterior process cannot possibly be descendants of other Stegocephalians in which the entopterygoids of both sides meet in a median suture and in which consequently the ethmoidal part of the parasphenoid and the posterior process of the vomer have been reduced.

9) The nervous system shows several important points of agreement in *Osteolepiformes*, *Labyrinthodontia* and *Anura*. The r. palatinus VII in the snout of *Lyrocephalus*, as far as known, had the course characteristic of *Osteolepiformes* and *Anura*, and the forebrain in *Lyrocephalus* and *Benthosuchus* was of the Osteolepiform—Anuran type.

Considering the above points and what has otherwise been set forth in this chapter, we are now justified in drawing the following conclusions concerning the relations between Crossopterygians, Stegocephalians and other Amphibians.

10) The *Labyrinthodontia* (including *Phyllospondyli*) and in all probability the *Ichthyostegidae* and at least several reptiles belong to the same common stock as *Osteolepiformes* and *Anura*. This stock (the *Eutetrapoda* of SÄVE-SÖDERBERGH plus the *Osteolepiformes*) branched into several lines.

11) One of these lines is represented by the *Ichthyostegidae* which became specialized quite early in a way indicating that they cannot have given rise to any later Tetrapods known to us.

12) The Carboniferous and Permian *Labyrinthodontia* known in detail are also specialized in several respects and undoubtedly represent several branches from the stock *Osteolepiformes—Anura*.

13) The majority of the Triassic Stegocephalians ("*Stereospondyli*" excluding Brachyopids and Plagiosaurids) retain a great many primitive Osteolepiform characters. They are in several respects intermediate between *Osteolepiformes* and *Anura*, though of course they do not include true transitional forms between these two groups.

14) The Stegocephalians known to us in detail do not include any forms representing the stock *Porolepiformes—Urodela*. It is not unthinkable, however, that certain imperfectly known Stegocephalians may belong to this stock. This applies above all to certain of the forms with a broad parasphenoid.

VI. Conclusions and summary.

This work treats of the snout in lower Gnathostomes with special reference to Crossopterygians. To facilitate comparisons between the various groups a uniform anatomical terminology is as far as possible introduced for the various skeletal elements and certain soft parts. Brief reviews are given of the structure of the snout in recent lower Gnathostomes, viz. Elasmobranchs, Brachiopterygians (*Polypterus*), Actinopterygians, Dipnoans, Urodeles and Anurans.

The main results gained and the conclusions drawn from these results may be briefly summarized as follows.

1) The following classification of the Crossopterygians has been given.

Crossopterygii.

I. Rhipidistia.
  A. *Porolepiformes.*
    1. Fam. *Porolepidae.*
    2. Fam. *Holoptychidae.*

  B. *Osteolepiformes.*
    1. Fam. *Osteolepidae.*
    2. Fam. *Rhizodontidae.*

II. Actinistia.
  A. *Coelacanthiformes.*
    1. Fam. *Coelacanthidae.*

2) In connection with the review of the structure of the snout in Dipnoans it is shown (pp. 273—280; fig. 13) a) that the subnasal cartilage in Dipnoans is part of the lateral nasal wall; b) that there is no true choana in Dipnoans; and c) that the opening generally regarded as a choana in Dipnoans is the posterior external nostril which has migrated downwards to the roof of the mouth and has become modified so as to resemble a choana.

3) The so-called septomaxillary in *Urodela* is a cartilage-bone (pp. 293—295, 402) and cannot be homologous to the septomaxillary in *Anura*, which is a dermal bone (pp. 317—319, 535). For this cartilage-bone in Urodeles the term nariodal is introduced (p. 249).

4) The general disposition of the sensory canal system of the snout in Crossopterygians is shown originally to have been very much the same in the three main groups of Crossopterygians (pp. 334—335). In Coelacanthids, however, it became more complicated through the development of several

anastomoses (pp. 336—339; fig. 32). The course of the supraorbital sensory canal in Coelacanthids in the suture between a medial and a lateral row of bones is a secondary condition (pp. 339—343).

5) A brief review is given of the general disposition of the dermal bones of the snout in Crossopterygians. It could be established that these bones are developed in fundamentally the same way in *Porolepiformes*, *Osteolepiformes* and *Coelacanthiformes* (pp. 346—353, figs. 33—35).

6) The bones in Crossopterygians previously known as antorbitals are here termed tectals (pp. 249, 351). The rostrals in Crossopterygians are on either side represented by one or more medial rostrals and a lateral rostral. All the rostrals are pierced by the infraorbital sensory canal. The nasals are never more than 7 in number. The postrostrals are very variable as to number and development. The bones in Postdevonian Coelacanthids previously interpreted as postrostrals are nasals. The medial rostral in *Porolepiformes* and *Osteolepiformes* is generally fused with the premaxillary into a rostro-premaxillary, which in these forms often includes also the foremost nasal element, thus making up a complex naso-rostro-premaxillary. The dermal bones of the ethmoidal shield in *Porolepiformes* and *Osteolepiformes* extend down onto the ventral face of the ethmoidal region and there form a marginal palatal lamina (pp. 353, 450). The vomer is paired and well developed in primitive members of all the main groups (pp. 352, 415, 450—451, 560, 583). In advanced Coelacanthids it is greatly reduced (p. 608). The parasphenoid extends far forwards underneath the ethmoidal region in *Osteolepiformes* and *Coelacanthiformes* (pp. 415, 492—493, 595). The ventral (palatal) face of the pars autopalatina of the palatoquadrate is covered by the dermopalatine (pp. 353, 453—454, 608—609) and the anterior part of the entopterygoid. In *Osteolepiformes* and certainly also in *Porolepiformes* the dermopalatine lies immediately behind the vomer, but at least in recent *Latimeria* among the *Coelacanthiformes* there is, between the vomer and the dermopalatine, an additional bone, the predermopalatine, which is situated underneath the ethmoidal region and covers the ventral face of a prearticular autopalatine part of the palatoquadrate (p. 608).

7) The snout of *Porolepiformes* is described in detail and is found to be of a characteristic type distinguished by the presence of a true choana and several other features.

8) The snout in *Osteolepiformes* is described in detail and is shown to be of a different type to that in *Porolepiformes*. The *Osteolepiformes* also possessed a true choana.

9) The snout in *Coelacanthiformes* is also thoroughly dealt with and it is established that it represents a third type, entirely different both

from that in *Porolepiformes* and from that in *Osteolepiformes*. There is no choana.

10) The snouts of Crossopterygians are thus referable to three different types, which according to the groups in which they are found may be referred to as a) the Porolepiform type, b) the Osteolepiform type, and c) the Coelacanthiform type.

11) The Porolepiform type of snout is distinguished inter alia by the following characters. The internasal wall is broad and houses both the foremost (ethmoidal) part of the cranial cavity and a large paired cavum internasale, which opens ventrally and also extends forwards into the divisio prenasalis communis and housed a paired intermaxillary gland. The nasal cavities lie far apart. They have very complete walls and each of them opens laterally through a small fenestra endonarina anterior and a small fenestra endonarina posterior and downwards into the mouth cavity through a likewise small fenestra endochoanalis situated in the postero-lateral corner of the solum nasi and continuous with the fenestra endonarina posterior. The postnasal wall is pierced by a very wide medial and several narrow lateral profundus canals. The tectum nasi is pierced by numerous canals for profundus branches. An orbito-rostral passage leads from the ventro-lateral part of the orbit forwards to the tip of the snout. The nasal cavity consists of a main chamber and a lateral recess. The lateral recess constitutes the hinder ventro-lateral part of the nasal cavity and is bounded ventrally by the solum nasi, laterally by the lateral nasal wall and dorsally by a horizontal crista rostro-caudalis. This crista is developed on the medial face of the lateral nasal wall, where it runs from close behind the ventral part of the fenestra endonarina anterior backwards to the fenestra endonarina posterior. During its passage backwards to the fenestra endonarina posterior the posterior external nasal tube lay just dorsally to the crista rostro-caudalis, in a groove in the medial face of the lateral nasal wall. The lateral recess is in open communication posteriorly with the mouth cavity. Its floor (a part of the solum nasi) is produced backwards into a small but very distinct process homologous to Seydel's palatal process. — The bulbus olfactorius lay ventro-laterally to the posterior part of the hemisphere. The n. profundus was very strongly developed. It divided into a medial, one or several lateral nasal branches and an orbitorostral branch in the orbit, that is to say before its entrance into the postnasal wall. The medial nasal branch was very strong and in the nasal cavity it broke up completely into numerous branches, the majority of which ascended to the dorso-medial parts of the roof of the snout. The lateral nasal branches and the orbitorostral branch of the nervus profundus supplied the lateral and anterior parts of the snout. The r. maxillaris V

was weakly developed and seems hardly to have gone forwards in front of the anterior end of the palatoquadrate. It cannot possibly have supplied more than a very short posterior ventro-lateral part of the snout. The lateral parts of the snout both received and were drained of their blood by vessels accompanying the profundus branches, i. e. by vessels that left or entered the orbit far medially. No large arteries or veins passed through the ventro-lateral parts of the snout. — The ethmoidal shield is pierced by a small fenestra exonarina anterior situated outside the fenestra endonarina anterior and of the same size as that. Between the ethmoidal shield and the lachrymal lies a small fenestra exonarina posterior. The lateral rostral has no process extending into the nasal cavity. The vomer possesses no descending tooth-bearing lamina and no posterior process. The vomers diverge forwards from each other and consequently there is between them a large anterior palatal fenestra in which opens the cavum internasale. The parasphenoid is broad and does not go sufficiently far forwards to cover any part of the internasal wall. — The palatoquadrate hardly extends forwards underneath the ethmoidal region, but articulates with the endocranium anteriorly a) in a fossa situated in the lower medial part of the posterior face of the postnasal wall and in an adjacent part of the lateral face of the interorbital wall, and b) against an area on the lateralmost ventral part of the posterior face of the postnasal wall.

12) The Osteolepiform type of snout is distinguished by the following principal characters. The internasal wall forms a septum nasi. It does not house either any part of the cranial cavity or any cavum internasale. The nasal cavities lie fairly close to each other. Each cavity opens laterally through a fenestra endonarina anterior and ventrally through a fenestra endochoanalis, both of which are fairly large. The fenestra endonarina posterior is situated in the postnasal wall and thus leads to the orbit. The postnasal wall is pierced by a single rather narrow profundus canal. Only one canal for profundus branches ascends from the nasal cavity. There is no orbitorostral passage. The divisio prenasalis communis is pierced by a branching canalis nasobasalis. The shape of the nasal cavity is fairly complicated. Its anterior and anterolateral parts are subdivided by a crista intermedia, a lamina superior, a strong inwardly directed processus intermedius from the lamina nariochoanalis of the lateral nasal wall, a strong inwardly directed processus dermintermedius from the lateral rostral, and a medial process of the anterior tectal, into a recessus superior, a recessus medius, and a recessus inferior. In addition the nasal cavity has two small recesses for the origin of the nasal muscles, a ventro-medial recess, which housed Jacobson's organ, and a lateral recess, which lies in the posterior con-

tinuation of the recessus inferior dorso-laterally to the fenestra endochoanalis and opens backwards into the mouth cavity. The lateral recess is bounded exclusively by the lateral nasal wall and its ventral medially curved part. There is thus no crista rostro-caudalis. — The posterior external nasal tube passed backwards from the nasal sac dorsally to the processus intermedius and the processus dermintermedius and then continued backwards above the lateral recess and through the fenestra endonarina posterior to the anterior lateralmost part of the orbit, where it ended in the orbital opening immediately in front of the eye. This tube was thus developed as a true naso-lachrymal duct. The bulbus olfactorius lay immediately in front of the hemisphere; it was short and probably fused with that of the opposite side. The n. olfactorius was fairly long. The n. profundus was not particularly strong and did not divide into a medial and a lateral nasal branch until in the postnasal wall. In the nasal cavity the medial nasal branch gave off a single dorsal branch, far anteriorly and near the medial end of the crista intermedia. It then passed downwards and forwards close to the medial end of the crista intermedia and left the nasal cavity at the anterior end of the medial part of the recessus inferior through the wide nasobasal canal which goes forwards through the prenasal wall to the foremost rostral part of the upper face of the ethmoidal region. In the nasobasal canal the nerve gave off a ventral terminal branch to the lower face of the divisio prenasalis communis and then broke up into a medial and a lateral terminal branch, which went to the rostral parts of the snout. The ventral terminal branch probably formed a prenasal anastomosis with the medial terminal branch of the r. palatinus VII. The n. profundus did not supply the anterior ventro-lateral parts of the snout to any large extent. The r. maxillaris V divided into four main branches, two of which, the r. palatonasalis and the r. infraorbitalis, went forwards into the ventro-lateral parts of the snout. The r. palatonasalis probably formed a prechoanal anastomosis with the antero-lateral terminal branch of the r. palatinus VII. The third branch formed a postchoanal anstomosis with the r. palatinus VII. The fourth branch divided into the rr. cutanei maxillares, which supplied the dermal bones and skin ventrolaterally to the orbit. The r. buccalis lateralis entered and traversed the lateral recess of the nasal cavity, then left the cavity and passed forwards to the tip of the snout along the ventro-lateral margin of the ethmoidal region. The r. palatinus VII pierced the vomer in a direction from above forwards and downwards and broke up into three terminal branches, medial, antero-lateral, and lateral. The lateral parts of the ethmoidal region both received and were drained of their blood by vessels accompanying the r. palatonasalis and the r. buccalis lateralis,

i. e. by vessels leaving or entering the anterior ventro-lateral part of the orbit. — The ethmoidal shield is pierced by a fairly small fenestra exonarina anterior. There is no separate fenestra exonarina posterior. The lateral rostral is provided with a large processus dermintermedius, which extends far into the nasal cavity and covers the dorsal face of the processus intermedius of the lamina nariochoanalis. The vomers do not diverge in front of the parasphenoid but meet in a median suture throughout their forward extent. Each vomer is provided with a strong descending tooth-bearing lamina, transverse in its anterior medial part, mainly rostro-caudal in its posterior lateral part, and a posterior process along the parasphenoid. Part of the ventral face of the divisio prenasalis communis is exposed in a broad but short median unpaired anterior palatal fenestra between the dermal bones. This fenestra lies in the roof of a well-defined fossa apicalis bounded anteriorly and laterally by the tooth-bearing parts of the premaxillaries and posteriorly by the anterior transverse parts of the descending tooth-bearing laminae of the vomers. A paired prenasal pit in the roof of the fossa apicalis housed the main portions of a paired intermaxillary gland. This pit is situated partly in the lower face of the part of the divisio prenasalis communis exposed in the anterior palatal fenestra, partly in the lower face of the vomer behind the said fenestra. The anterior transverse parts of the descending tooth-bearing laminae of the vomers meet in a more or less complete median suture. In the anterior face of their median parts, i. e. in the anterior face of the posterior wall of the fossa apicalis, is a median unpaired intervomerine pit, which opens backwards behind the fossa apicalis just below the anterior tip of the parasphenoid through a median unpaired intervomerine canal (sometimes represented by a foramen between the tooth-bearing laminae of the vomers). The intervomerine pit and canal were in all probability developed for the common efferent duct of the paired intermaxillary gland. The parasphenoid is narrow and extends forwards underneath the ethmoidal region about to the transition of the internasal wall into the divisio prenasalis communis. — The palatoquadrate hardly extends forwards underneath the ethmoidal region. It was rigidly connected with the ethmoidal region at the ventro-medial part of the posterior face of the postnasal wall, but further laterally it lay underneath and was in contact with the lower face of the postnasal wall. — The oblique muscles of the eye arose close together on the ventro-medial part of the posterior face of the postnasal wall. The m. levator bulbi was differentiated inter alia into a portio principalis and a portio transversalis, which arose on the lateral face of the interorbital wall and were inserted into the dorsal face of the pars autopalatina of the palatoquadrate and into a pit between the pars autopalatina and the postnasal wall respectively.

13) The Coelacanthiform type of snout may be characterized as follows. The internasal wall is comparatively narrow ventrally but widens considerably dorsally, where it houses a closed median rostral cavity representing the ethmoidal part of the cranial cavity in embryos of lower Gnathostomes. The postnasal wall is very thick and extends far forwards. Its antero-lateral part has a paired large fossa ventro-lateralis opening antero-latero-ventrally. Owing to the thickness of the postnasal wall the nasal cavities lie comparatively far forwards in the ethmoidal region. Most ventrally the nasal cavities are fairly close to each other but further dorsally they are fairly far apart. There is no fenestra endochoanalis and thus no choana. The lateral nasal wall is perforated by a large fenestra endonarina communis. The nasal cavity is of a simple shape. It consists of a main chamber, an antero-medial recess and a small postero-dorso-lateral recess. — The long and high bulbi olfactorii lay in front of the hemispheres in the posterior parts of the canales olfactorii and were separated from each other throughout. The n. olfactorius was short. The n. profundus entered the nasal cavity but does not seem to have divided into medial and lateral nasal branches. The r. maxillaris V and the r. buccalis lateralis passed forwards through the ventro-lateral part of the fossa ventro-lateralis. In front of that they entered the nasal cavity close behind or through the postero-ventral corner of the fenestra endonarina communis and traversed the ventro-lateral part of the nasal cavity. The dorsal parts of the snout received and were drained of blood by an ophthalmic artery and an ophthalmic vein accompanying the r. ophthalmicus lateralis. The main vessels of the ventro-lateral parts of the snout were presumably a maxillary artery and an infra-orbital vein accompanying the r. buccalis lateralis and the r. maxillaris V. A special canal leading from the ventro-medial part of the posterior face of the postnasal wall to the canalis olfactorius probably housed an orbitonasal artery, but since it is wide and continues forwards to open into the anterior part of the profundus canal, it was probably also traversed by some other structure, presumably a vein from the nasal cavity. Apart from the fossa ventro-lateralis the palatal face of the snout presents no special depressions, fossae or cavities, and there are thus no traces of an intermaxillary gland. — The ethmoidal shield is pierced by a fenestra exonarina anterior and two fenestrae exonarinae posteriores on either side. It has no palatal lamina. The lateral rostral is as a whole tube-shaped and covers the ventral part of the fenestra endonarina communis from the outside. It is provided with a superficial antero-dorsal process, which is pierced by the anterior transverse com-

missural sensory canal. The antero-dorsal process does not extend inwards into the nasal cavity but is situated outside the part of the fenestra endonarina communis from which issue the anterior and posterior external nasal tubes, just behind the proximal part of the anterior tube. The posterior external nasal tube passed backwards and divided into two branches with separate outward openings. Consequently there were two posterior external nostrils situated between the nasal cavity and the eye. The vomer possesses no tooth-bearing lamina. The parasphenoid is broad and extends far forward underneath the ethmoidal region. A predermopalatine is present. — The sensory canal system is fundamentally as in other Crossopterygians but becomes complicated in Postdevonian forms by the development of several anastomoses. The infraorbital sensory canal is situated far dorsally along the lateral face of the postnasal wall, and there runs in a curve concave ventrally. — The palatoquadrate extends fairly far forwards underneath the ethmoidal region and articulates against the lower face of the postnasal wall, postero-medially and medially to the fossa ventro-lateralis. At least in certain forms it has a prearticular autopalatine part which covers the ventral face of the ethmoidal region between the vomer and the autopalatine articular facet. Its pars autopalatina has an ascending lamina, which occupied the fossa ventro-lateralis. The maxillary is greatly reduced or absent. — The places of origin of the oblique muscles of the eye are widely separated and there is both a dorsal and a ventral anterior myodome.

14) The snout in *Polypterus* approaches in most respects the Coelacanthiform type (pp. 598—612). Both as to the snout and otherwise *Polypterus* differs so considerably from Actinopterygians that it cannot be referred to them. As it cannot either be referred to the Coelacanthids (p. 612), it has together with the closely allied *Calamoichthys* been placed in a group of its own, *Brachiopterygii* Stensiö 1921.

15) The *Actinopterygii* are fairly variable as regards the snout. They are, however, most closely comparable to *Brachiopterygii* and *Coelacanthiformes* (pp. 612—619).

16) The snout in *Dipnoi* is greatly modified and differs considerably from that in all other forms. As pointed out in 2, the posterior external nostril in Dipnoans has become transformed into a pseudo-choana and there is no true choana.

17) The snout in *Urodela* is of the Porolepiform type and agrees also in several details almost completely with that in *Porolepiformes* (pp. 417—421). It differs from that in *Porolepiformes* mainly in two respects: the development of the skeleton is much less complete and the palatoquadrate is fused with the endocranium.

18) The snout in *Anura* is of the Osteolepiform type and

agrees in most details almost exactly with that in *Osteolepiformes* (pp. 550—554). It differs from that in *Osteolepiformes* essentially only in the much less complete development of the skeleton.

19) The snout at least in the vast majority of *Stegocephalia* is of the Osteolepiform type (pp. 639—640). The lateral rostral (septomaxillary) in all Stegocephalians known in any detail is fundamentally as in *Osteolepiformes* (pp. 623—625). The Triassic "*Stereospondyli*", excluding Brachyopids and Plagiosaurids, agree particularly well with *Osteolepiformes* with regard to the development of the anterior part of the palate (pp. 627—637).

20) The external nostril in the Devonian *Ichthyostegidae* is an anterior external nostril which has secondarily shifted down to the lower side of the snout (p. 622). The Ichthyostegids represent an early side-branch from the Stegocephalian stock.

21) The snout at least in certain primitive *Reptilia* is of the Osteolepiform type, the septomaxillary being developed as in *Osteolepiformes* (pp. 625—626).

22) Though greatly different, the Porolepiform and Osteolepiform types of snout are far more closely related to each other than to the Coelacanthiform type. The snout in *Porolepiformes* and *Osteolepiformes* has in fundamental features reached the same stage as in primitive Tetrapods, whereas the snout in *Coelacanthiformes* in all respects remains in a typical fish stage. The snout in *Porolepiformes* and *Osteolepiformes* is thus much more highly specialized in several respects than the Coelacanthid snout. This refers above all to the presence of a true choana. The development of the choana in *Porolepiformes* and *Osteolepiformes* has obviously led to considerable modifications of the whole snout in these two groups. There is thus reason to assume that the snout in *Coelacanthiformes* has retained at least several primitive characters of the common ancestral Crossopterygian from which *Porolepiformes*, *Osteolepiformes* and Coelacanthids have arisen. As these primitive Crossopterygians must have been closely allied to the ancestors of *Brachiopterygii* and *Actinopterygii*, it is easily understood that the snout in Coelacanthids in several characters resembles the snout in these two groups of fishes.

23) The skeleton of the snout is very well ossified and very completely developed in *Porolepiformes*, *Osteolepiformes* and primitive *Coelacanthiformes*, but to a large extent cartilaginous and reduced in *Urodela*, *Anura* and advanced *Coelacanthiformes* (pp. 422, 526, 551, 592—593, 595). Both in *Porolepiformes*, *Osteolepiformes* and primitive *Coelacanthiformes* the ethmoidal region and the orbitotemporal region are occupied by a large unpaired ethmosphenoid, which extends forward to the very tip of the

ethmoidal region. In *Porolepiformes* and *Osteolepiformes* the palatoquadrate is also occupied throughout by a single ossification, whereas in *Coelacanthiformes* there is an independent autopalatine ossification. In *Urodela* and *Anura* the ossification in the endocranial part of the snout is confined to an unpaired orbitosphenoid or sphenethmoid situated in the anterior parts of the interorbital wall and sometimes extending forwards into the hinder parts of the ethmoidal region. In addition we find a cartilage-bone, the nariodal bone, in the lateral nasal wall of certain *Urodela*. Both in Urodeles and Anurans the endoskeleton of the snout has also to a large extent become entirely reduced. In all Postdevonian *Coelacanthiformes* there is a paired ethmoidal ossification, which has about the same extent in Palaeozoic forms as in recent *Latimeria* (p. 593).

24) The lateral rostral in *Osteolepiformes* is a true homologue of the septomaxillary in Anurans, Stegocephalians and primitive reptiles. In the *Osteolepiformes* (pp. 449—450) it consists of three parts: a) a facial part covering part of the outside of the lateral nasal wall; b) a processus dermintermedius which extends far into the nasal cavity and covers the dorsal face of the processus intermedius of the lamina nariochoanalis; and c) a processus palatinus which lies on the ventral face of the ethmoidal region. The septomaxillary in *Anura* corresponds to the processus dermintermedius but may at least sometimes have also a small facial part (pp. 529—535). The septomaxillary in Stegocephalians may be provided with the same three parts as the lateral rostral in *Osteolepiformes*, but mostly it seems to consist only of a facial part and a processus dermintermedius (p. 625). The septomaxillary in at least certain primitive reptiles consists of a pars facialis, a processus dermintermedius and a pars palatina (p. 626).

25) The intermaxillary gland was present in *Porolepiformes* (pp. 400—401), *Osteolepiformes* (pp. 505—506), and at least in most Stegocephalians (pp. 629, 634). This gland was situated in the same way in *Porolepiformes* as in *Urodela*, but in *Osteolepiformes* and *Stegocephalia* its position corresponded to that in *Anura*.

26) The posterior external nasal tube is the homologue of the ductus nasolacrimalis in Tetrapods (pp. 402, 446—447, 513, 627). In *Osteolepiformes* it went backwards to the orbital opening and was already modified into a true nasolachrymal duct.

27) The nasolachrymal duct was situated dorsally to the processus dermintermedius in *Osteolepiformes*. Also in *Anura* it originally lay dorsally to the processus dermintermedius (the septomaxillary) but then migrated down through that bone in connection with the downward widening of the recessus medius of the nasal cavity (pp. 514, 518, 537—539).

28) No Stegocephalians are known with certainty to belong to the *Porolepiformes—Urodela* stock (p. 639).

29) The vast majority of Stegocephalians and at least certain primitive reptiles belong to the *Osteolepiformes—Anura* stock.

30) It is obvious from the results gained in this work that *Porolepiformes* and *Osteolepiformes* represent two quite different lines of evolution. It has long been known that the Rhipidistid Crossopterygians must be closely related to the Amphibians. Since it is now obvious that as regards the snout *Porolepiformes* are as Urodeles, whereas *Osteolepiformes* agree with Anurans, it follows that the Amphibian ancestors very early divided into a *Porolepiformes—Urodela* stock and an *Osteolepiformes—Anura* stock. Everything would thus appear to bear out the opinion that the Amphibians are a diphyletic group, the Urodeles being derived from primitive *Osteolepiformes* whereas the Anurans have developed from primitive *Osteolepiformes.* The present investigations have thus corroborated the opinions advanced by Wintrebert (1922), Holmgren (1933, 1939), Säve-Söderbergh (1934, 1936) and Herre (1935, p. 70) that Urodeles and Anurans have arisen independently of each other.

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Printed $^{17}/_{11}$ *1942.*

PLATES

Plate 1.

Porolepis spitsbergensis n. sp.

Holotype. Imperfect anterior part of the divisio cranialis anterior. Palaeontological Museum, Oslo. Unknown locality. Wood Bay, Spitzbergen. Wood Bay Series (Lower Devonian). Figured by Stensiö in 1932 (fig. 30 A_1).

Fig. 1. Left half of holotype in ventral view. A lateral part removed so that the lower face of the tectum nasi is seen. The foremost part of the nasal cavity and the left cavum internasale also shown. 4/1.

Fig. 2. Lateral part of the left nasal capsule with the cast of the nasal cavity in medial and somewhat dorsal view. 4/1.

Fig. 3. Holotype in lateral view (left side). 2/1.

Fig. 4. Holotype in posterior view. 2/1.

Fr-eth.sh, fronto-ethmoidal shield; c_a*or,* anterior canal of orbitorostral passage; *cav.in,* cavum internasale; *c.o.lat,* canal for r. ophthalmicus lateralis; *c.olf,* canalis olfactorius; *c.prd, c.prdl,* canals, probably for dorsal and dorso-lateral branches of n. profundus; *c.prm,* medial profundus canal; *c.prt,* canals for terminal twigs of medial terminal profundus branch; *c.cut.va?,* canal for branch of n. profundus, possibly also for cutaneous vessel; *c.vadl,* canal directed dorso-laterally, probably mainly for vessels; c_1*prdm,* c_2*prdm,* canals for dorso-medial profundus branches; c_1*prl,* lateral profundus canal; *div.fbr,* forebrain division of cranial cavity; *eth.cr,* ethmoidal part of cranial cavity: *fe.exa,* fenestra exonarina anterior; *fe.vl,* fenestra ventro-lateralis; *gr.olf,* groove for n. olfactorius; *i.exp,* notch in the margin of ethmoidal shield for posterior nasal tube; *od.La,* area of fronto-ethmoidal shield overlapped by lachrymal; *pr.S,* Seydel's palatal process; *pr.vl,* ventro-lateral process of postnasal wall; *re.bulb,* recess for bulbus olfactorius; *ri.w.al,* crista rostro-caudalis; *te.n,* tectum nasi; *w.mn,* medial nasal wall; *w.pn,* postnasal wall; *w.pren,* divisio prenasalis communis.

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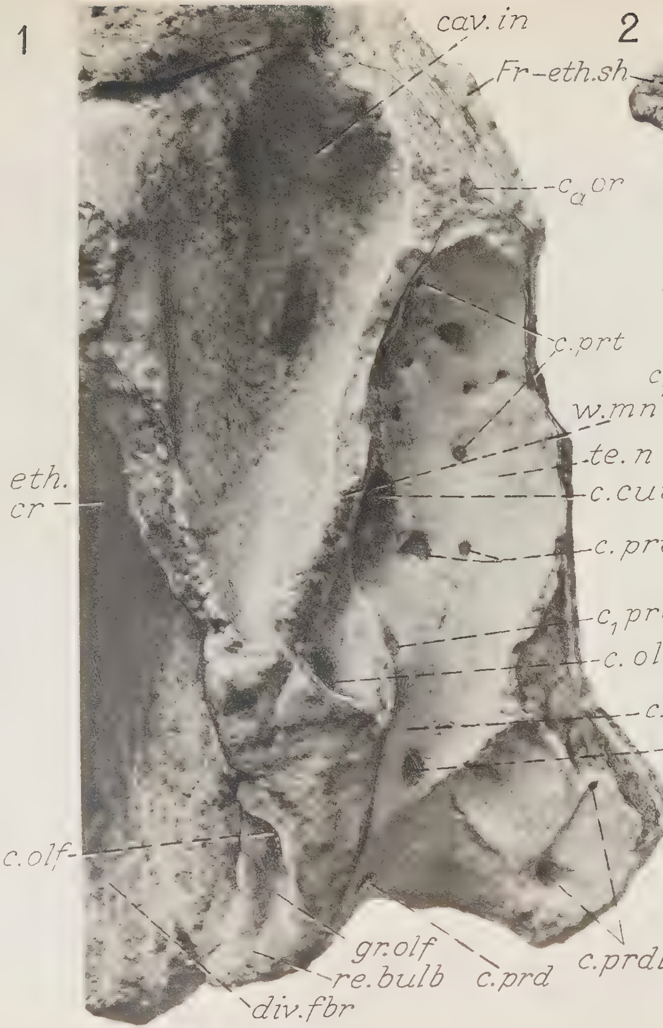
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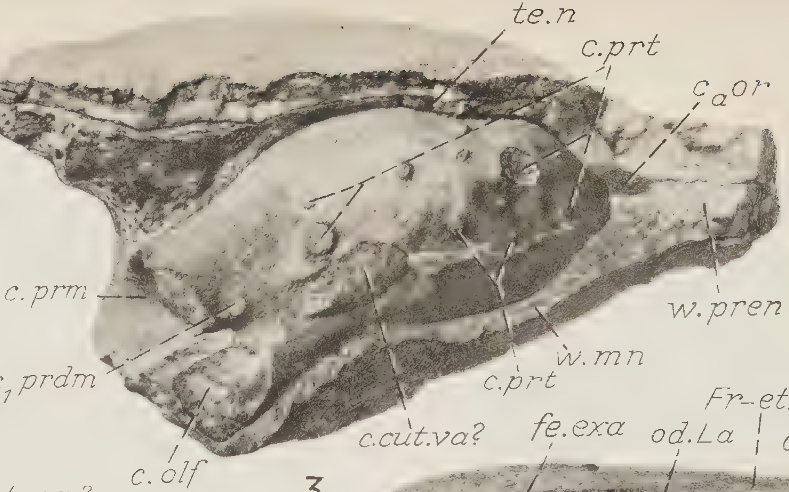
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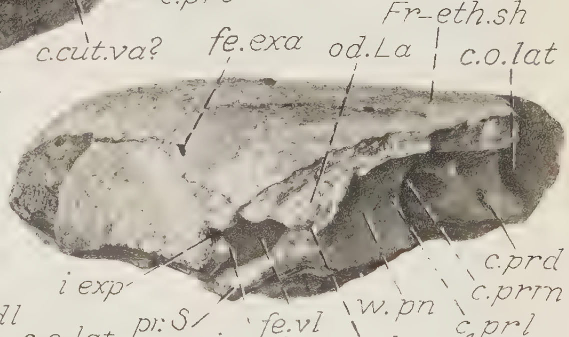
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4

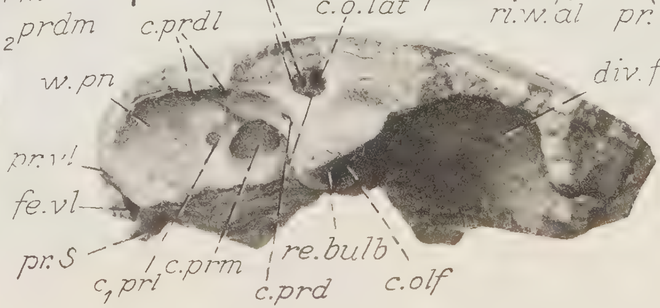
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Plate 2.

Fig. 1. *Porolepis brevis* n. sp. Part of the divisio cranialis anterior in antero-lateral view. Specimen E.—N.—S. No. 216. Mt. Kronprintz, W. slope, Bock Bay, Spitzbergen. Wood Bay Series (Lower Devonian). 7/1.

Fig. 2. *Porolepis spitsbergensis* n. sp. Holotype in postero-ventro-lateral view. The postero-latero-ventral part of the ethmoidal region with the fenestra ventro-lateralis well shown. Same specimen as in pl. 1. 4/1.

Fig. 3. *Porolepis spitsbergensis* n. sp. Holotype in ventral view. Same specimen as in fig. 2 and in pl. 1. 2/1.

Fr-eth.sh, fronto-ethmoidal shield; *ar.Vo*, vomeral area; *cav.in*, cavum internasale; *c.olf*, canalis olfactorius; *c.prd*, *c.prdl*, canals, probably for dorsal and dorso-lateral branches of n. profundus; *c.prm*, medial profundus canal; *c.prt*, canals for terminal twigs of medial terminal profundus branch; c_1prdm, c_2prdm, canals for dorso-medial profundus branches; c_1prl, lateral profundus canal; *div.fbr*, forebrain division of cranial cavity; *eth.cr*, ethmoidal part of cranial cavity; *fe.ena*, fenestra endonarina anterior; *fe.exa*, fenestra exonarina anterior; *fe.vl*, fenestra ventro-lateralis; *gr.ntp*, groove for posterior nasal tube; *gr.olf*, groove for n. olfactorius; *i.enp*, notch in the margin of fenestra ventro-lateralis for posterior nasal tube; *i.exp*, notch in the margin of ethmoidal shield for posterior nasal tube; *iocp*, pores of infraorbital sensary canal; *la.pal* lamina palatina of ethmoidal shield; *od.La*, area of fronto-ethmoidal shield overlapped by lachrymal; *od.La* + *Mx*, area of ethmoidal shield overlapped by lachrymal and maxillary; *pmxt*, premaxillary tooth; *pr.S*, Seydel's palatal process; *pr.vl*, ventro-lateral process of postnasal wall; *re.bulb*, recess for bulbus olfactorius; *re.l*, lateral recess of nasal cavity; *ri.in*, internasal ridge; *ri.w.al*, crista rostro-caudalis; *sol.n*, solum nasi; *te.o*, tectum orbitale; *w.mn*, medial nasal wall; *w.pn*, postnasal wall.

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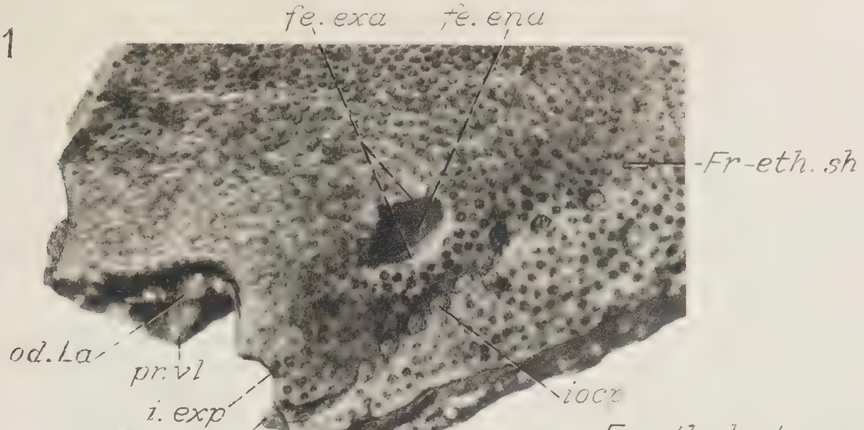
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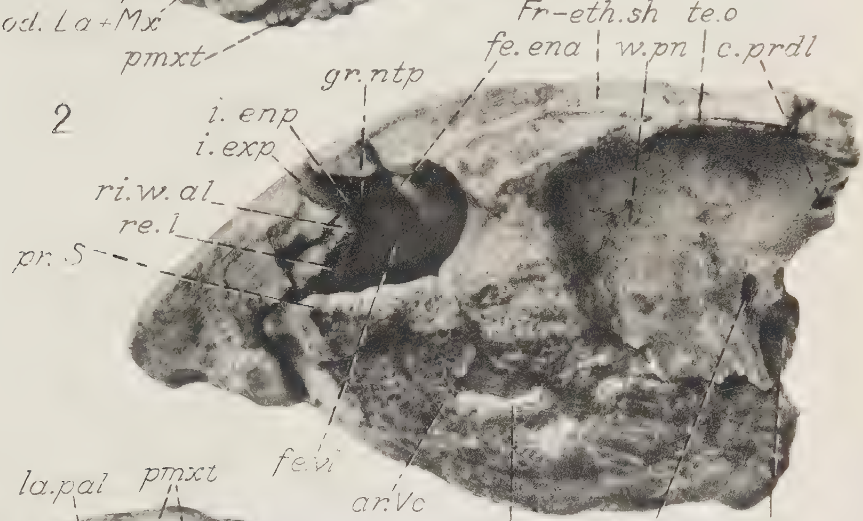
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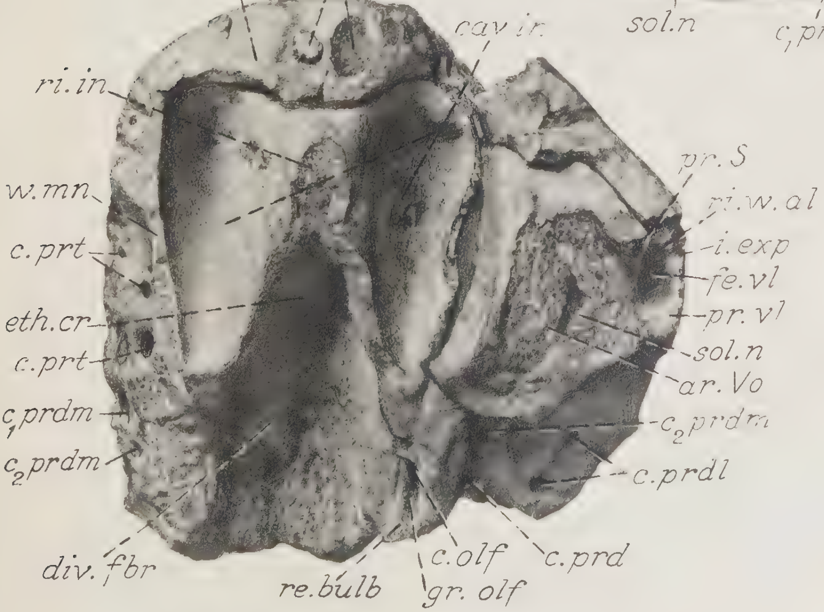
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Plate 3.

Porolepis brevis n. sp.

Fig. 1. Holotype. The divisio cranialis anterior in posterior view. Chiefly the ethmosphenoid as seen from behind. Specimen E.—N.—S. No. 214. Mt. Kronprintz, Bock Bay, Spitzbergen. Wood Bay Series (Lower Devonian). 4/1.

Fig. 2. The divisio cranialis anterior in ventral view. Same specimen as in pl. 2, fig. 1. 4/1.

Fig. 3. Ventro-lateral part of the right side of the snout in postero-ventral view. Hinder parts of lateral rostral and (naso-rostro-)premaxillary partly in section. Part of the ethmoidal region and ethmoidal shield removed to show the nasal cavity. Specimen E.—N.—S. No. 268. Mt. Kronprintz, opposite Stjör valley, Wood Bay, Spitzbergen. Wood Bay Series (Lower Devonian). 4/1.

Pmx_1, Pmx_3, pars dentalis and pars palatina of premaxillary; *Psph*, parasphenoid; *R.l.pal*, pars palatina of lateral rostral; *art.aup?*, area against which pars autopalatina probably abutted; *ar.Vo*, vomeral area; $c_a or$, $c_p or$, anterior and posterior canals of orbitorostral passage; *cav.cr*, cranial cavity; *cav.in*, cavum internasale; *cav.nc*, cavity of nasal capsule; *c.o.lat*, canal for r. ophthalmicus lateralis; *c.prm*, medial profundus canal; *cr.susp*, crista suspendens; *c.vl*, canal piercing ventro-lateral part of postnasal wall; $c_1 prl$, $c_2 prl$, lateral profundus canals; *fe.ena*, fenestra endonarina anterior; *fe.exa*, fenestra exonarina anterior; *fe.vl*, fenestra ventro-lateralis; *fo.aup*, autopalatine fossa; *fo.chd*, pit in posterior face of ethmosphenoid representing anterior end of chordal canal; *gr.ntp*, groove for posterior nasal tube; $gr_p or$, posterior groove of orbitorostral passage; *gr.So + Po*, groove in lateral margin of fronto-ethmoidal shield, occupied by medial margins of supraorbital and postorbital; *ioc*, infraorbital sensory canal; *od.La*, area of fronto-ethmoidal shield overlapped by lachrymal; *od. La + Mx*, area of ethmoidal shield overlapped by lachrymal and maxillary; *om*, margin of orbital opening; *pmxt*, premaxillary tooth; *pr.bp*, basipterygoid process; *pr.conn*, processus connectens; *pr.S*, Seydel's palatal process; *pr.vl*, ventro-lateral process of postnasal wall; *re.l*, lateral recess of nasal cavity; *ri.in*, internasal ridge; *ri.olf*, olfactory ridge; *ri.w.al*, crista rostro-caudalis; *sol.n*, solum nasi; *w.al*, (antero-)lateral nasal wall; *w.pn*, postnasal wall; *w.po*, postorbital wall.

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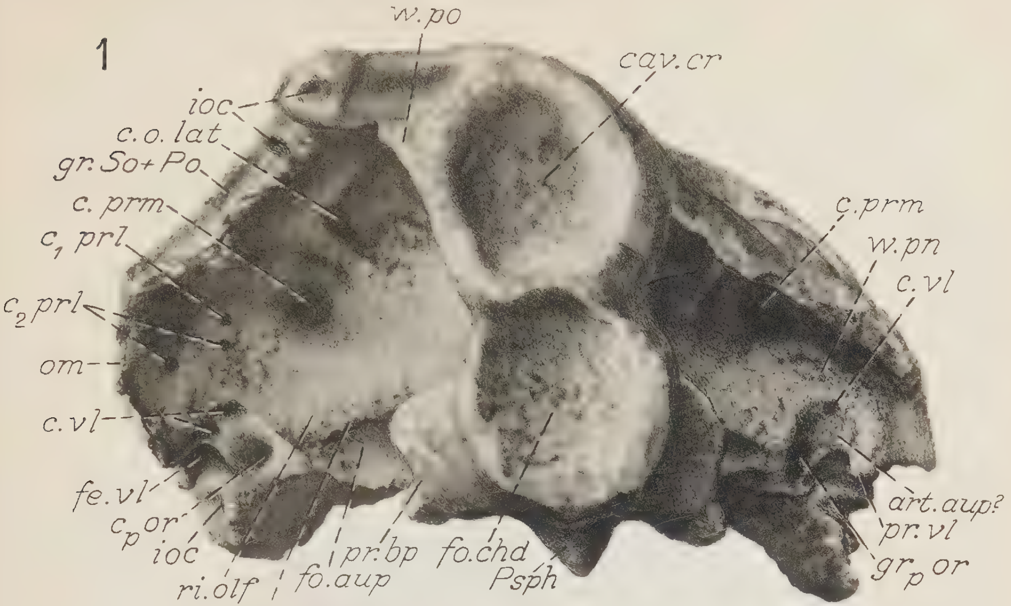
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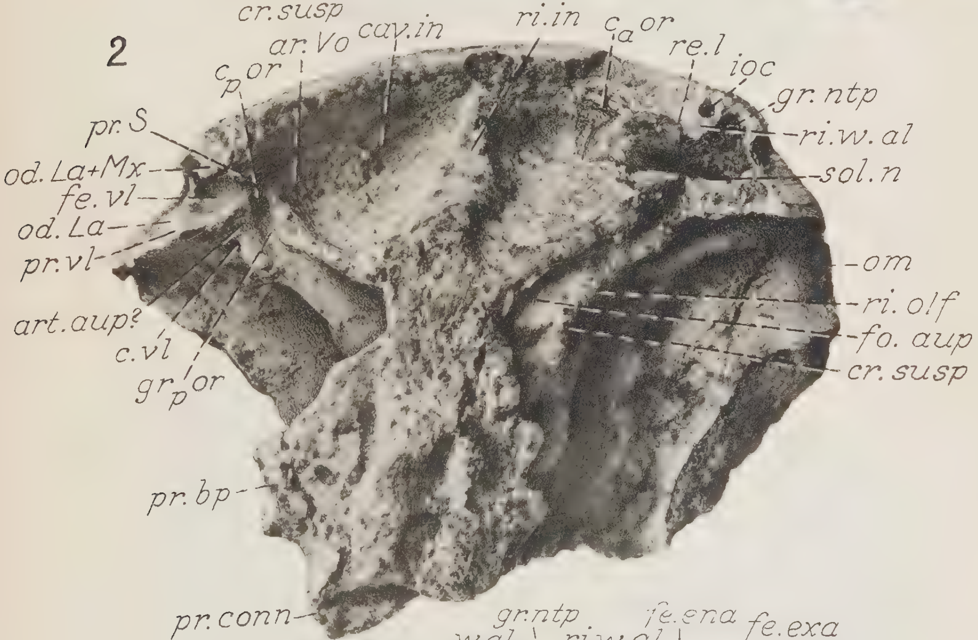
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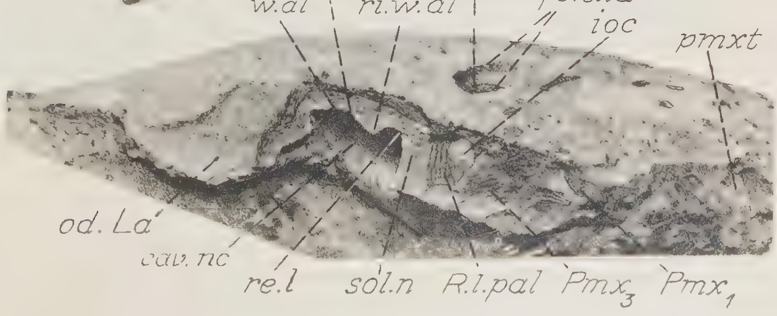
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R.l.pal
Pmx_3
Pmx_1

Plate 4.

Porolepis brevis n. sp.

Holotype, figured also in pl. 3, fig. 1.
Fig. 1 in ventral view. 4/1.
Fig. 2 from the right side. 4/1.

Etsph, ethmosphenoid; *Fr-eth.sh*, fronto-ethmoidal shield; *Psph*, parasphenoid; *art. aup?*, area against which pars autopalatina probably abutted; *ar.Vo*, vomeral area; *cav.in*, cavum internasale; *c.o.lat*, canal for r. ophthalmicus lateralis; $c_{p}or$, posterior canal of orbitorostral passage; *cr.susp*, crista suspendens; *c.vl*, canal piercing ventro-lateral part of postnasal wall; $c_{2}prl$, lateral profundus canal; *fe.exa*, fenestra exonarina anterior; *fe.vl*, fenestra ventro-lateralis; *fo.aup*, autopalatine fossa; *fo.chd*, pit in posterior face of ethmosphenoid representing anterior end of chordal canal; $gr_{p}or$, posterior groove of orbitorostral passage; *i.exp*, notch in margin of ethmoidal shield for posterior nasal tube; *ioc*, infraorbital sensory canal; *iocp*, pores of infraorbital canal; *od.La*, area of fronto-ethmoidal shield overlapped by lachrymal; *od.La + Mx*, area of ethmoidal shield overlapped by lachrymal and maxillary; *pmxt*, premaxillary tooth; *pr.bp*, basipterygoid process; *pr.conn*, processus connectens; *pr.vl*, ventro-lateral process of postnasal wall; *ri.in*, internasal ridge; *ri.olf*, olfactory ridge; *ri.soc*. supraorbital sensory canal ridge; *te.o*, tectum orbitale; *w.po*, postorbital wall.

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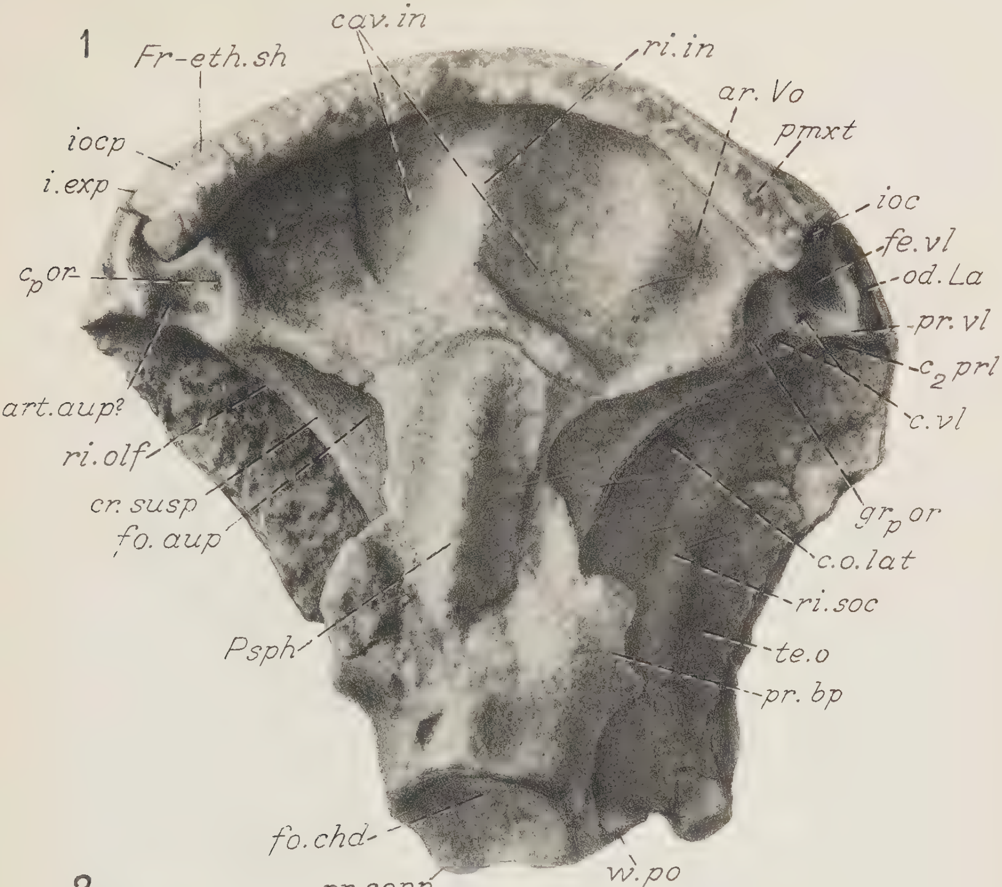
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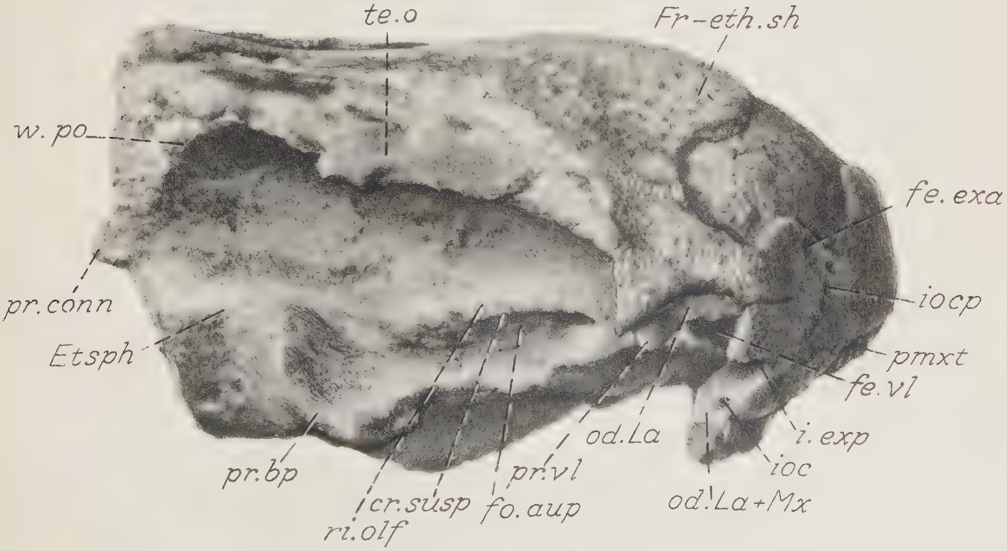
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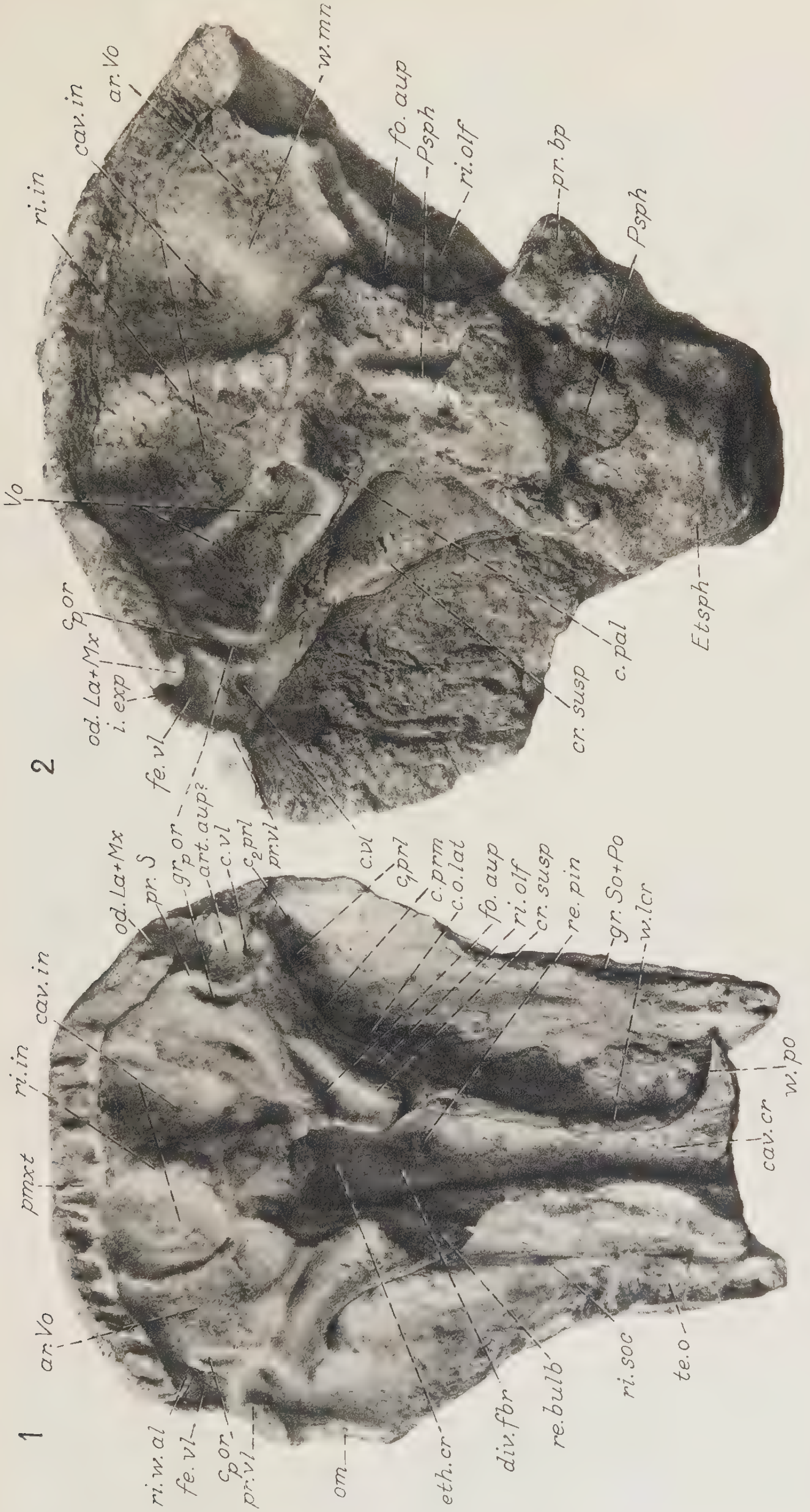
cr.susp
fo.aup
od.La+Mx
ri.olf

Plate 5.

Fig. 1. *Porolepis elongata* n. sp. Holotype. Imperfect divisio cranialis anterior. Ventral view. Specimen E.—N.—S. No. 229. Mt. Kronprintz, W. slope, Bock Bay, Spitzbergen. Wood Bay Series (Lower Devonian). 3/2.

Fig. 2. *Porolepis* cf. *brevis* n. sp. A fairly complete divisio cranialis anterior. Ventral view. Specimen E.—N.—S. No. 22. Mt. Sigurd, E. slope, Wood Bay, Spitzbergen. Wood Bay Series (Lower Devonian). 3/2.

Etsph, ethmosphenoid; *Psph*, parasphenoid; *Vo*, vomer; *art. aup?*, area against which pars autopalatina probably abutted; *ar.Vo*, vomeral area; *cav.cr*, cranial cavity (diencephalic division); *cav.in*, cavum internasale; *c.o.lat*, canal for r. ophthalmicus lateralis; *c.pal*, canal for r. palatinus VII; $c_{p}or$, posterior canal of orbitorostral passage; *c.prm*, medial profundus canal; *cr.susp*, crista suspendens; *c.vl*, canal piercing ventro-lateral part of postnasal wall; $c_{1}prl$, $c_{2}prl$, lateral profundus canals; *div.fbr*, forebrain division of cranial cavity; *eth.cr*, ethmoidal part of cranial cavity; *fe.vl*, fenestra ventro-lateralis; *fo.aup*, autopalatine fossa; $gr_{p}or$, posterior groove of orbitorostral passage; *gr.So + Po*, groove in lateral margin of fronto-ethmoidal shield occupied by the medial margins of supraorbital and postorbital; *i.exp.* notch in margin of ethmoidal shield for posterior nasal tube; *od.La + Mx*, area of ethmoidal shield overlapped by lachrymal and maxillary; *om*, margin of orbital opening; *pmxt*, premaxillary tooth; *pr. bp*, basipterygoid process; *pr. S*, Seydel's palatal process; *pr.vl*,ventro-lateral process of postnasal wall; *re.bulb*, recess for bulbus olfactorius; *re.pin*, recess for pineal organ; *ri.in*, internasal ridge; *ri.olf*, olfactory ridge; *ri.soc*, supraorbital sensory canal ridge; *ri.w.al*, crista rostro-caudalis; *te.o*, tectum orbitale; *w.lcr*, lateral wall of cranial cavity; *w.mn*, medial nasal wall; *w.po*, postorbital wall.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i.exp
fe.vl
cr.susp
c.pal
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cav.in
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w.po
cav.cr
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ri.soc
re.bulb
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Plate 6.

Fig. 1. *Eusthenopteron foordi* Whiteaves. Snout in anterior view. Specimen No. P. 341, Palaeozoological Department of the Swedish Museum of Natural History, Stockholm. 3/1.

Fig. 2. *Eusthenopteron foordi* Whiteaves. Right lateral part of snout in antero-lateral aspect. A foremost part of the palatoquadrate also shown. Specimen PATTEN Coll. No. F. 5, Dartmouth College, Hanover, N. H. U. S. A. 4/1.

Fig. 3. *Porolepis* sp. Ventral part of the left nasal capsule with certain dermal bones. Dorsal view. The solum nasi seen from above. Specimen E.—N.—S. No. 451. The mountain nearest to the N. of Mt. Garborg, Ekman Bay, Spitzbergen. Wood Bay Series (Lower Devonian). 4/1.

Fr-eth.sh, fronto-ethmoidal shield; Na_{2+3}, compound nasal formed by fusion of nasals 2 and 3; NRP_1, NRP_2, pars dentalis and pars facialis of naso-rostro-premaxillary; Pmx_1, pars dentalis of premaxillary; *Ptr*, postrostral; *R.l*, lateral rostral; *So-Te*, supraorbito-tectal; *Te.a*, anterior tectal; *Vo*, vomer; art_2l, art_2m, lateral and medial ethmoidal articular areas; $c_{al}pal$, antero-lateral branch of palatine canal; $c_{a}or$, anterior canal of orbitorostral passage; $c_{l}pal$, lateral branch of palatine canal; $c_{p}or$, posterior canal of orbitorostral passage; *c.iv*, intervomerine canal; c_1prl, lateral profundus canal; *c.Pmx*, canal for nerve to premaxillary teeth; *fe.ena*, fenestra endonarina anterior; *fe.exa*, fenestra exonarina anterior; *fo.ap*, fossa apicalis; *fo.iv*, intervomerine pit; $gr_{a}or$, anterior groove of orbitorostral passage; *gr.ntp*, groove for posterior nasal tube; *ioc*, infraorbital sensory canal; ioc_c, ethmoidal commissure of the infraorbital sensory canals; *iocp*, pore of infraorbital sensory canal; $i_{mp}.tr$, notch forming medial wall of pit, probably for insertion of portio transversalis of m. levator bulbi; *la.pal*, lamina palatina of ethmoidal shield; *la.Vo*, vertical tooth-bearing lamina of vomer; $od.La + Mx$, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *pr.ap*, processus apicalis of pars autopalatina; *pr.dim*, processus dermintermedius of lateral rostral; $pr.dim_{rc}$, anterior, recurved portion of processus dermintermedius; *pr.Te*, medial process of anterior tectal extending into nasal cavity; *re.m.ln*, recess for m. lateralis narium; *ri.Psph*, tooth-bearing ridge of parasphenoid; *ri.w.al*, crista rostro-caudalis; *soc*, supraorbital sensory canal; *sol.n*, solum nasi; *w.al*, (antero-)lateral nasal wall; *vot*, vomerine tusk; *w. pren*, divisio prenasalis communis.

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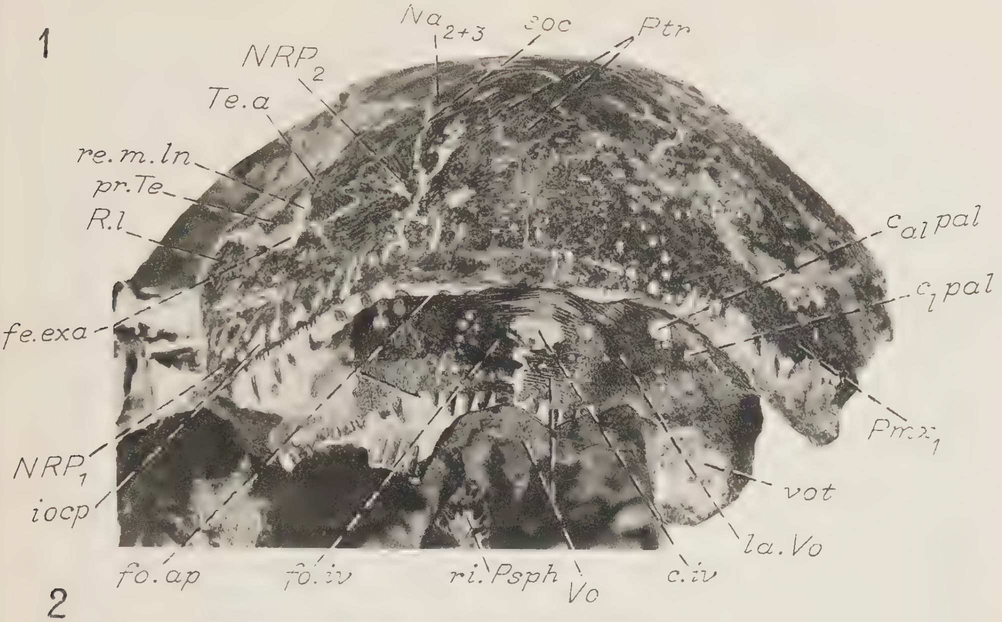
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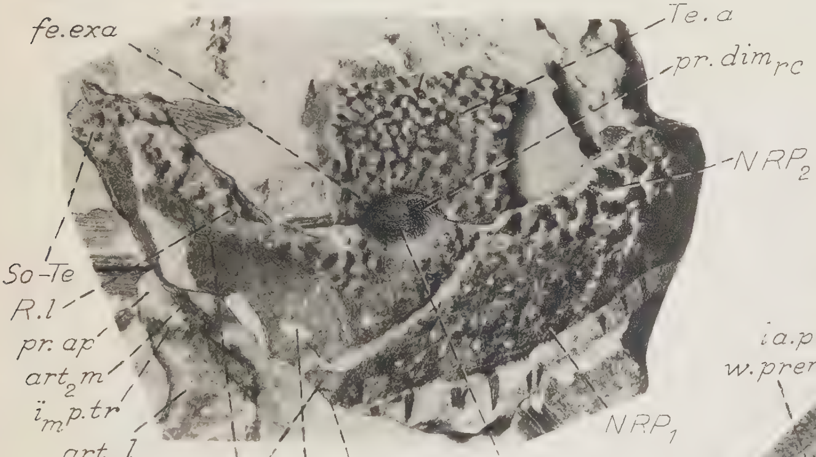
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Te.a
$pr.dim_{rc}$
NRP_2
So-Te
R.l
pr.ap
art_2m
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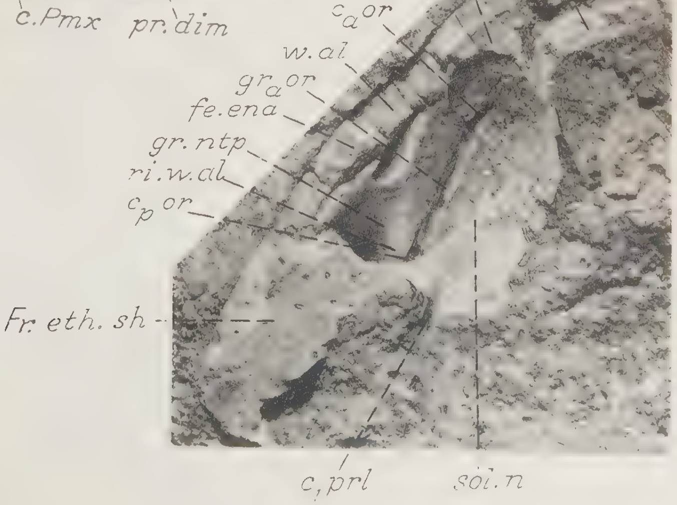
art_2l
od.La+Mx
ioc
c.Pmx
pr.dim
NRP_1

3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w.al
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fe.ena
gr.ntp
ri.w.al
$c_p or$
Fr. eth. sh
$c_1 prl$
soi.n

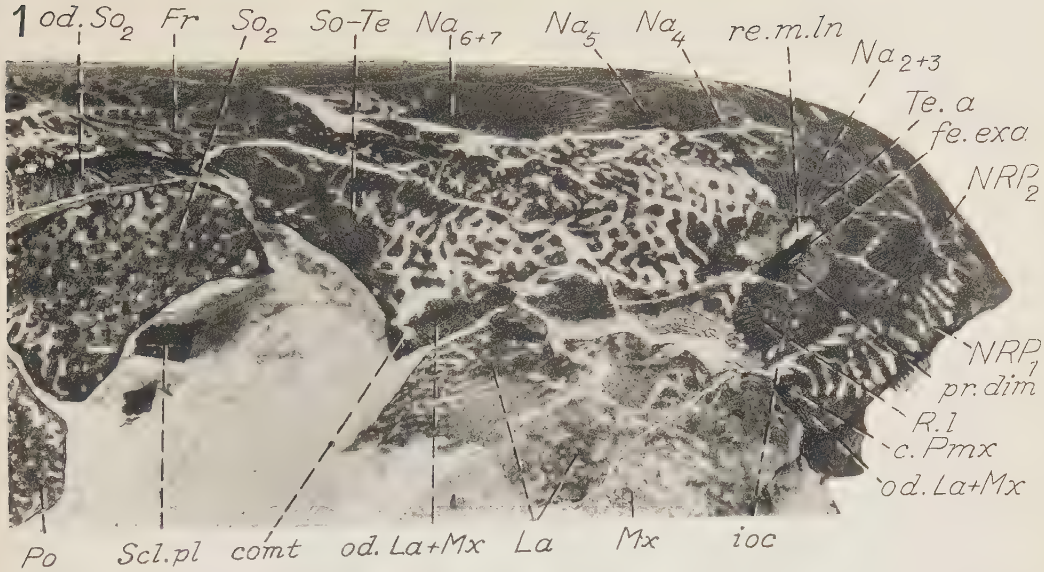
Plate 7.

Eusthenopteron foordi Whiteaves.

Anterior parts of the fronto-ethmoidal shield with an anterior part of the cheek. 3/1. Specimen No. P. 341, Palaeozoological Department of the Swedish Museum of Natural History, Stockholm. Same specimen as in pl. 6, fig. 1, pl. 8, figs. 1—3, and pl. 9, figs. 2 and 3. Fig. 1 lateral view. Fig. 2 dorsal view.

Fr, frontal; *La*, lachrymal; *Mx*, maxillary; Na_{2+3}, compound nasal formed by fusion of the nasals 2 och 3; Na_4, Na_5, nasals 4 and 5; Na_{6+7}, compound nasal formed by fusion of nasals 6 and 7; NRP_1, NRP_2, pars dentalis and pars facialis of compound naso-rostro-premaxillary of right side (on the left side of this specimen, as seen on the palatal side, pl. 8, fig. 1, the premaxillary and the medial rostral are independent); *Po*, postorbital; *Ptr*, postrostrals; Ptr_m, posterior median postrostral; *R.l*, lateral rostral (pars facialis); *Scl.pl*, sclerotic plate; So_2, posterior supraorbital; *So-Te*, supraorbito-tectal; *Te.a*, anterior tectal; *cart*, area of endocranium probably slightly ossified or cartilaginous; *comt*, tube of infraorbital sensory canal, which enters the supraorbito-tectal and forms a commissure between the supraorbital and infraorbital sensory canals; $c_7o.lat$, branch of canal for r. ophthalmicus lateralis, probably for a nerve branch to canal organ in nasal 7; *c.o.lat*, canal for r. ophthalmicus lateralis; *c.Pmx*, canal for nerve to premaxillary teeth; *c.perf*, canal for r. frontalis perforans of n. profundus; *fe.exa*, fenestra exonarina anterior; *gr.soc*, groove for supraorbital sensory canal ridge; *ioc*, infraorbital sensory canal; $od.La+Mx$, area of the fronto-ethmoidal shield overlapped by lachrymal and maxillary; $od.So_2$, area of frontal overlapped by posterior supraorbital; *pr.dim*, processus dermintermedius of lateral rostral; *re.m.ln*, recess for m. lateralis narium; *soc*, supraorbital sensory canal.

1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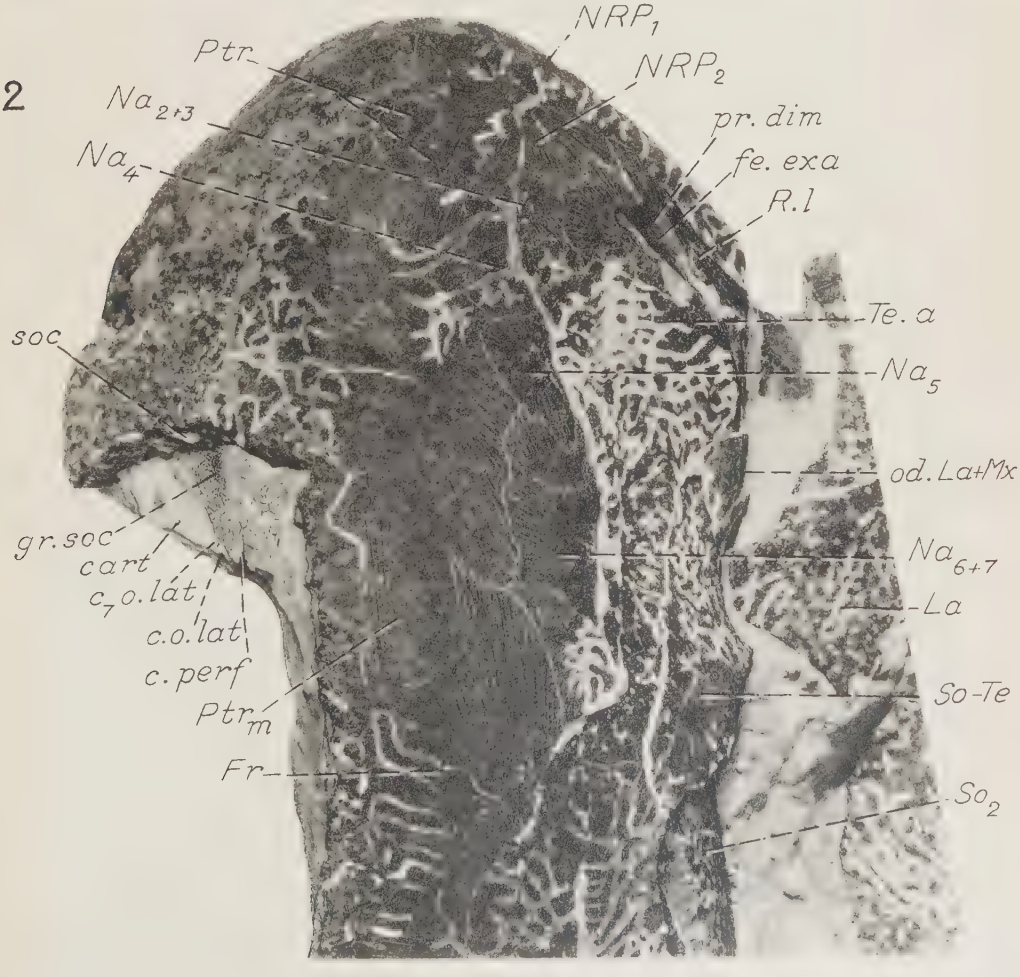
So_2
So-Te
Na_{6+7}
Na_5
Na_4
re.m.ln
Na_{2+3}
Te. a
fe. exa
NRP_2
NRP_1
pr. dim
R. l
c. Pmx
od. La+Mx
Po
Scl.pl
comt
od. La+Mx
La
Mx
ioc

2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NRP_2
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Na_4
fe. exa
R. l
Te. a
soc
Na_5
od. La+Mx
gr.soc
cart
Na_{6+7}
c_7 o. lat
La
c. o. lat
c. perf
So-Te
Ptr_m
Fr
So_2

Plate 8.

Eusthenopteron foordi Whiteaves.

Specimen No. P. 341, Palaeozoological Department of the Swedish Museum of Natural History, Stockholm. Same specimen as in pl. 7.

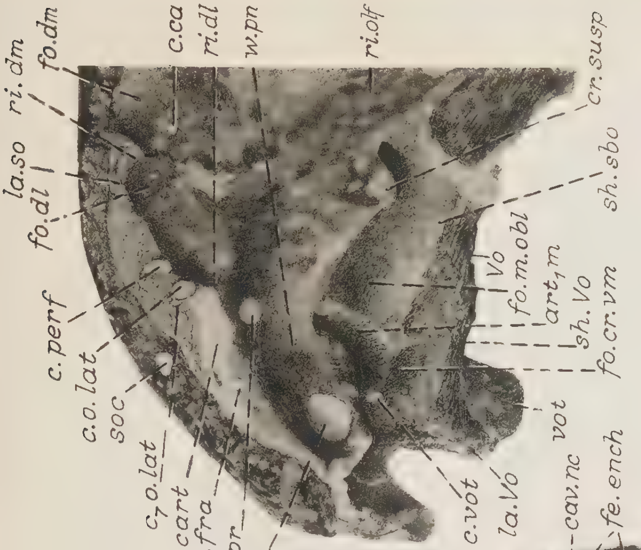
Fig. 1. Anterior part of the divisio cranialis anterior and anterior part of the right palatoquadrate complex in ventral view. 4/1.

Fig. 2. Left side of ethmoidal region with dermal bones in postero-lateral view.

Fig. 3. A lateral part of the left vomer with an adjacent part of the ethmoidal shield in antero-medial view. 4/1.

Aup, pars autopalatina; *Dpl*, dermopalatine; *Enpt*, entopterygoid; NRP_1, pars dentalis of compound naso-rostro-premaxillary of the left side; Pmx_1, Pmx_3, pars dentalis and pars palatina of premaxillary; *Psph*, parasphenoid; *R.l*, lateral rostral; *R.l.pal*, processus palatinus of lateral rostral; *R.m.pal*, processus palatinus of medial rostral; *Vo*, vomer; art_1m, medial autopalatine articular area; $c_{al}pal$, antero-lateral branch of palatine canal; $c_{ap}\text{-}n$, anterior palatonasal canal; *cart*, superficial part of endocranium probably formed of cartilage; *cav.nc*, nasal cavity; *c.ca*, canal for v. cerebralis anterior; *c.fra*, canal for r. frontalis anterior of n. profundus; *c.iv*, intervomerine canal; c_lpal, c_mpal, lateral and medial branches of palatine canal; $c.NRP_3$, canals piercing pars palatina of the naso-rostro-premaxillary; *c.o.lat*, canal for r. ophthalmicus lateralis; *c.perf*, canal for r. frontalis perforans of n. profundus; *c.Pmx*, canal for nerve to premaxillary teeth; *c.pr*, profundus canal; *cr.susp*, crista suspendens; $c_vn\text{-}b$, ventral branch of nasobasal canal; *c.vot*, canal for branch of postchoanal nerve anastomosis to vomerine tusks; $c_7o.lat$, canal for branch of r. ophthalmicus lateralis to canal organ in nasal 7; *fe.ench*, fenestra endochoanalis; *fe.enp*, opening, probably representing fenestra endonarina posterior; *fe.exch*, fenestra exochoanalis; *fe.pal*, anterior palatal fenestra; *fo.ap*, fossa apicalis; *fo.cr.vm*, pit receiving the ventro-medial crista of pars autopalatina; *fo.dl*, *fo.dm*, dorso-lateral and dorso-medial depressions in posterior face of postnasal wall; *fo.iv*, intervomerine pit; *fo.m.obl*, pit for origin of oblique eye muscles; *fo.pren*, prenasal pit; *fo.vot*, pit of missing vomerine tusk; *ioc*, infraorbital sensory canal; *la.pal*, lamina palatina of ethmoidal shield; *la.so*, lamina supraorbitalis; *la.Vo*, ventral tooth-bearing lamina of vomer; pr_lNRP_3, lateral process of pars palatina of naso-rostro-premaxillary or lateral paired process of palatal lamina of ethmoidal shield; pr_mNRP_3, medial process of pars palatina of naso-rostro-premaxillary or lateral half of median unpaired process of palatal lamina of ethmoidal shield; *pr.Vo*, antero-lateral process of vomer; *ri.dl*, *ri.dm*, dorso-lateral and dorso-medial ridges on posterior face of postnasal wall and adjacent part of lateral face of interorbital wall; *ri.olf*, olfactory ridge; *ri.Psph*, ventral tooth-bearing ridge of parasphenoid; *sh.sbo*, anterior suborbital ledge; *sh.Vo*, vomerine shelf; *soc*, supraorbital sensory canal; *w.pn*, postnasal wall; *vot*, vomerine tusk.

2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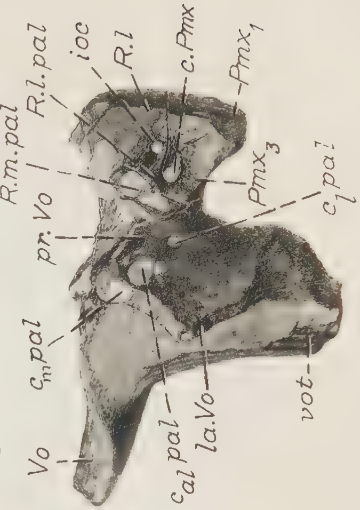
la.Vo

3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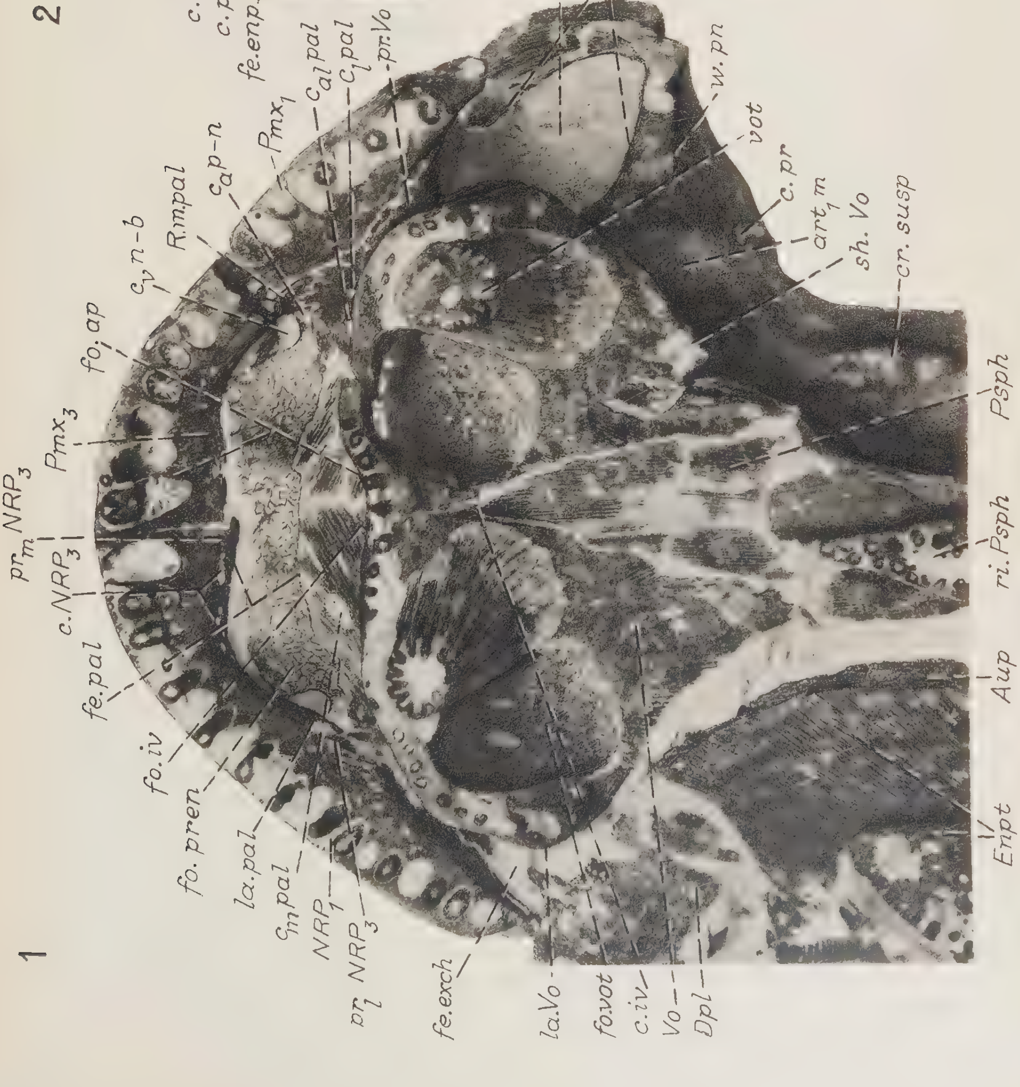
la.Vo
vot

1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pr.Vo
cav.nc
fe.ench
w.pn
vot
c.pr
art_1m
sh.Vo
cr.susp
Psph
ri.Psph
Aup
Enpt
c.NRP_3
fe.pal
fo.iv
fo.pren
la.pal
$c_m$pal
NRP_1
pr_l NRP_3
fe.exch
la.Vo
fo.vot
c.iv
Vo
Dpl

Plate 9.

Eusthenopteron foordi Whiteaves.

Fig. 1. Deficient snout seen from the left side and slightly from in front. Same specimen as in pl. 6, fig. 2 and pl. 10, fig. 1. 3/1.

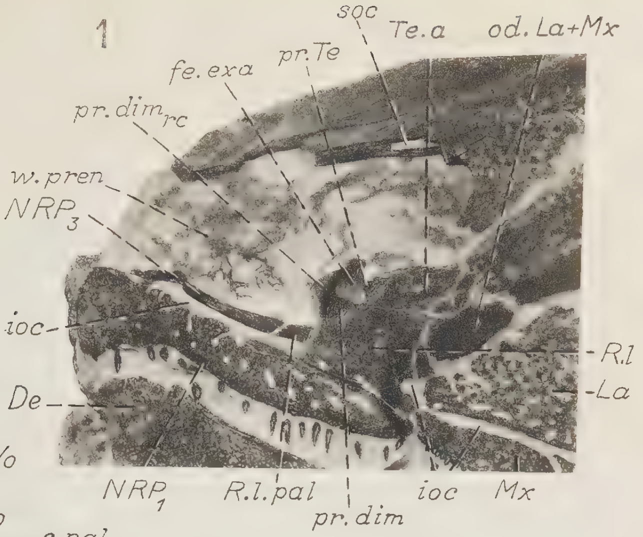
Fig. 2. A lateral part of the left vomer with an adjacent part of the ethmoidal shield in dorsal view. Same piece as in pl. 8, fig. 3. 4/1.

Fig. 3. Part of the left half of the ethmoidal region seen from below. Several of the dermal bones partly preserved in position. Same specimen as in pl. 8, fig. 1, but with the piece shown in pl. 8, fig. 3 and in pl. 9, fig. 2 removed. 4/1.

Fig. 4. Parts of a snout in anterior view. Considerable parts are missing on the right side (left in the figure) so that the vomers are exposed from in front. Specimen No. P. 383, Palaeozoological Department of the Swedish Museum of Natural History, Stockholm. 7/1.

De, dentary; *La*, lachrymal; *Mx*, maxillary; NRP_1, NRP_3, pars dentalis and pars palatina of naso-rostro-premaxillary; Pmx_1, Pmx_3, pars dentalis and pars palatina of independent premaxillary; *R.l*, lateral rostral; *R.m.pal*, *R.l.pal*, processus palatinus of lateral and medial rostrals; *Te.a*, anterior tectal; *Vo*, vomer; art_1m, medial autopalatine of articular area; $c_{al}pal$, antero-lateral branch of palatine canal; $c_{a}p\text{-}n$, anterior palatonasal canal; *cav.nc*, nasal cavity; *c.buc*, canal for r. buccalis lateralis; $c_{m}pal$, medial branch of palatine canal; *c.n-b*, nasobasal canal; *co.pm*, postero-ventro-medial corner of ethmoidal region; *c.pal*, palatine canal; *c.Pmx*, canal for nerve to premaxillary teeth; *c.pr*, profundus canal; *cr.sbn*, crista subnasalis; *cr.susp*, crista suspendens; $c_{v}n\text{-}b$, ventral branch of nasobasal canal; *c.vot*, canal for branch of postchoanal nerve anastomosis to vomerine tusks; *fe.ench*, fenestra endochoanalis; *fe.exa*, fenestra exonarina anterior; *fo.ap*, fossa apicalis; *gr.pal*, groove on dorsal face of vomer for r. palatinus VII; *ioc*, infraorbital sensory canal; *la.pal*, palatal lamina of ethmoidal shield; *la.Vo*, vertical tooth-bearing lamina of vomer; $od.La + Mx$, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *pr.dim*, processus dermintermedius of lateral rostral; $pr.dim_{rc}$, anterior recurved portion of processus dermintermedius; *pr.Te*, medial process of the anterior tectal extending into nasal cavity; *pr.Vo*, antero-lateral process of vomer; $ri.NRP_3$, dorsal ridge on pars palatina of naso-rostro-premaxillary; *soc*, supraorbital sensory canal; *sol.n*, solum nasi; vot_1, vot_2, antero-medial and postero-lateral tusk of right vomer; *w.pn*, postnasal wall; *w.pren*, divisio prenasalis communis.

1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w.pren
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La
De
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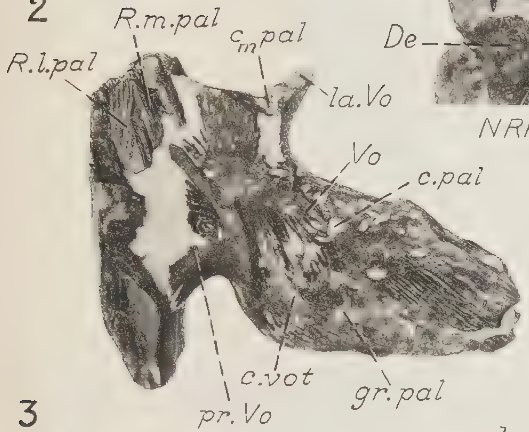
R.l.pal
pr.dim
ioc
Mx

2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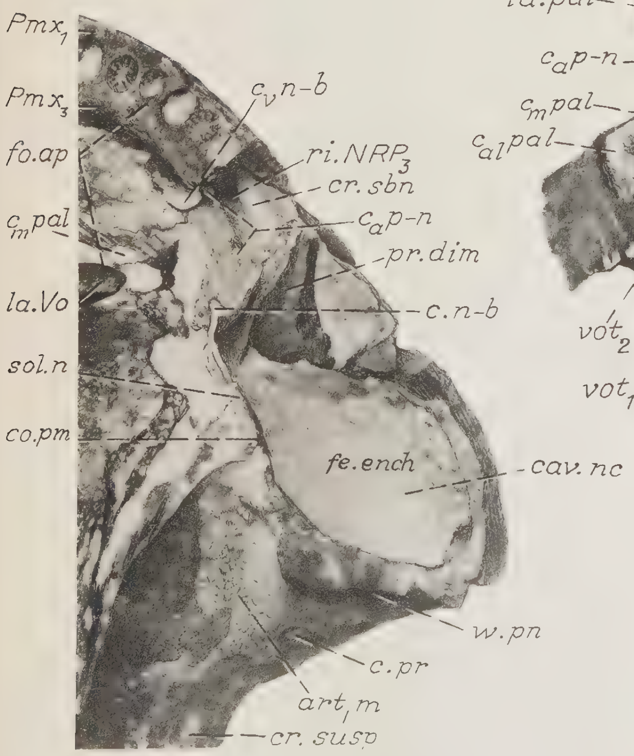
3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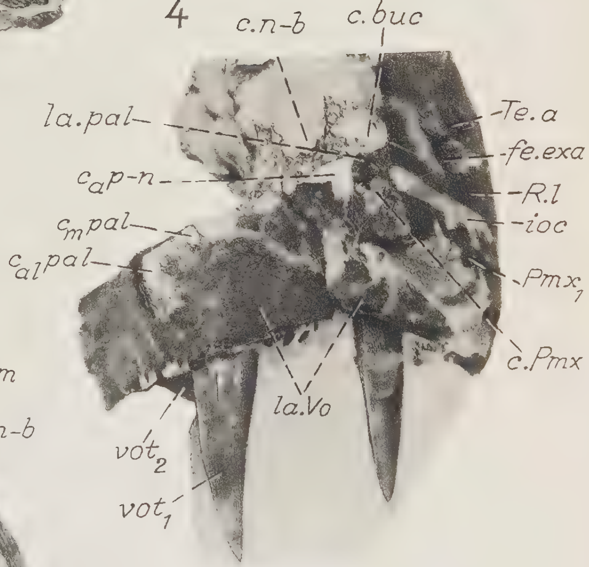
w.pn
c.pr
art$_1$m
cr. susp

4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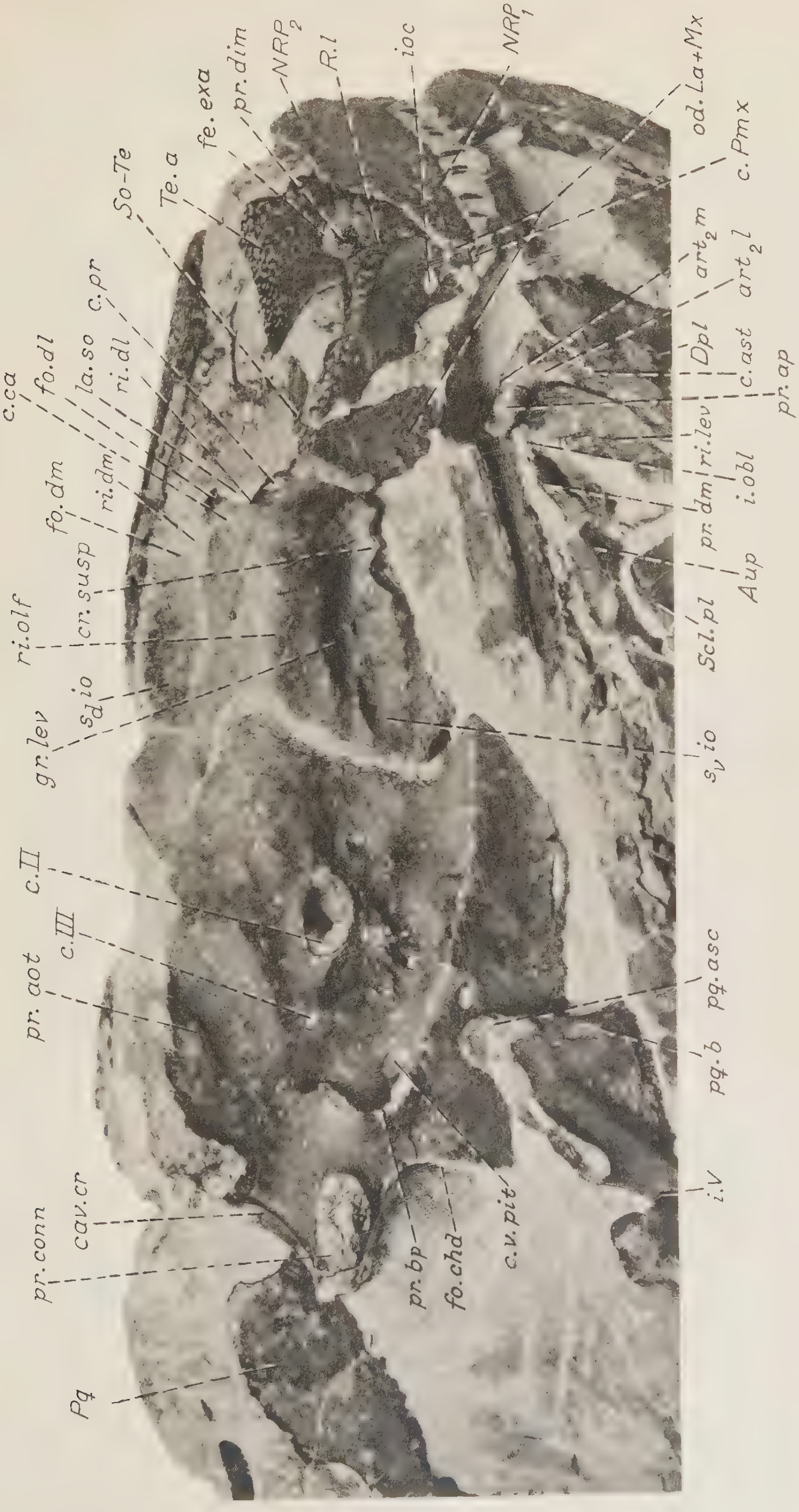
ioc
c$_{al}$pal
Pmx$_1$
c.Pmx
la.Vo
vot$_2$
vot$_1$

Plate 10.

Eusthenopteron foordi Whiteaves.

Specimen with the divisio cranialis anterior prepared so as to show the larger posterior part of the ethmosphenoid. Lateral view. Specimen Patten Coll. No. F. 5, Dartmouth College, Hanover, N. H., U. S. A. Same specimen as in pl. 6, fig. 2 and pl. 9, fig. 1. 3/1.

Aup, pars autopalatina of palatoquadrate; *Dpl*, dermopalatine; NRP_1, NRP_2, pars dentalis and pars facialis of naso-rostro-premaxillary; *Pq*, palatoquadrate of left side; *R.l*, lateral rostral; *Scl.pl*, sclerotic plate; *So-Te*, supraorbito-tectal; *Te.a*, anterior tectal; art_2l, art_2m, lateral and medial ethmoidal articular areas; *cav.cr*, cranial cavity; *c.ast*, canal for postchoanal anastomosis; *c.ca*, canal for v. cerebralis anterior; *c.Pmx*, canal for nerve to premaxillary teeth; *c.pr*, profundus canal; *cr.susp*, crista suspendens; *c.v.pit*, canal for pituitary vein; *c.II*, canal for n. opticus; *c.III*, canal for n. oculomotorius; *fe.exa*, fenestra exonarina anterior; *gr.lev*, groove for origin of principal portion of m. levator bulbi; *fo.chd*, pit in posterior face of ethmosphenoid, representing anterior end of the chordal fossa; *fo.dl*, *fo.dm*, dorsolateral and dorso-medial depressions in posterior face of postnasal wall; *i.obl*, notch for oblique eye muscles; *ioc*, infraorbital sensory canal; *i.V*, notch in dorsal margin of palatoquadrate for n. trigeminus; *la.so*, lamina supraorbitalis; *od.La + Mx*, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *pq.asc*, *pq.b*, parts of palatoquadrate on the medial side of which are found the processus ascendens and basalis; *pr.aot*, antotic process; *pr.ap*, processus apicalis of pars autopalatina; *pr.bp*, basipterygoid process; *pr.conn*, processus connectens; *pr.dim*, processus dermintermedius of lateral rostral; *pr.dm*, dorso-medial process of pars autopalatina; *ri.dl*, *ri.dm*, dorso-lateral and dorso-medial ridges on posterior face of postnasal wall and on adjacent part of lateral face of interorbital wall; *ri.lev*, ridge for insertion of principal portion of m. levator bulbi; *ri.olf*, olfactory ridge; $s_{d}io$, $s_{v}io$, thin dorsal and ventral parts of interorbital wall.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c.Pmx
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art_2l
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pr.ap
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pr.dm
i.obl
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s_vio
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c.III
pr.aot
pg.asc
pg.b
i.V
cav.cr
pr.conn
pr.bp
fo.chd
c.v.pit
Pq

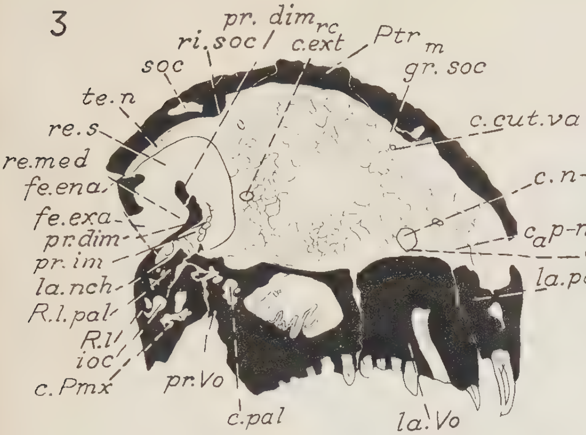
Plate 11.

Eusthenopteron foordi Whiteaves.

Six transverse sections through the anterior part of the snout. 5/2. Figs. 1—5. Sections Nos. 72, 61, 47, 42 and 31 of grinding-series 1. Fig. 6. Section No. 20 of grinding-series 2.

NRP_3, pars palatina of naso-rostro-premaxillary; Pmx_1, Pmx_3, pars dentalis and pars palatina of premaxillary; Ptr_m, posterior median postrostral; *R.l*, lateral rostral; *R.l.pal*, processus palatinus of lateral rostral; *Te.a*, anterior tectal; *Vo*, vomer; c_a*p-n*, anterior palatonasal canal; *cav.nc*, nasal cavity; *c.buc*, canal for r. buccalis lateralis; *c.cut.va*, canal for cutaneous vessel; *c.ext*, canal for r. externus narium of n. profundus; c_l*n-b*, c_m*n-b*, lateral and medial branches of nasobasal canal; *c.n-b*, nasobasal canal; *c.pal*, palatine canal; *c.Pmx*, canal for nerve to premaxillary teeth; $c_{R.l}$*buc*, canal for branch of r. buccalis lateralis to canal organ in lateral rostral; *cr.sbn*, crista subnasalis; c_v*n-b*, ventral branch of nasobasal canal; *fe.ena*, fenestra endonarina anterior; *fe.ench*, fenestra endochoanalis; *fe.exa*, fenestra exonarina anterior; *fe.pal*, anterior palatal fenestra; *fo.ap*, fossa apicalis; *fo.pren*, prenasal pit; *fo.vot*, pit of missing vomerine tusk; *gr.mn*, groove for r. medialis narium; *gr.pal*, groove on dorsal face of vomer for r. palatinus VII; *gr.soc*, groove for supraorbital sensory canal ridge; *ioc*, infraorbital sensory canal; *la.nch*, lamina nariochoanalis; *la.pal*, lamina palatina of ethmoidal shield; *la.Vo*, vertical tooth-bearing lamina of vomer; *pr.dim*, processus dermintermedius of lateral rostral; $pr.dim_{rc}$, anterior recurved portion of processus dermintermedius; *pr.im*, processus intermedius of lamina nariochoanalis; *pr.Te*, medial process of anterior tectal extending into nasal cavity; *pr.Vo*, antero-lateral process of vomer; *re.i*, *re.med*, recessi inferior and medius of nasal cavity; *re.m.ln*, recessus for m. lateralis narium; *re.s*, *re.vm*, recessi superior and ventro-medialis of nasal cavity; ri_c*ioc*, ridge on dorsal face of pars palatina of naso-rostro-premaxillary lodging ethmoidal commissure of infraorbital sensory canals; $ri.NRP_3$, ridge on dorsal face of pars palatina of naso-rostro-premaxillary; *ri.soc*, supraorbital sensory canal ridge; *sn*, septum nasi; *soc*, supraorbital sensory canal; *sol.n*, solum nasi; *te.n*, tectum nasi; *vot*, vomerine tusk.

3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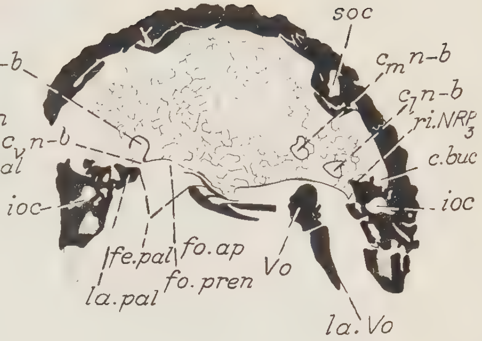
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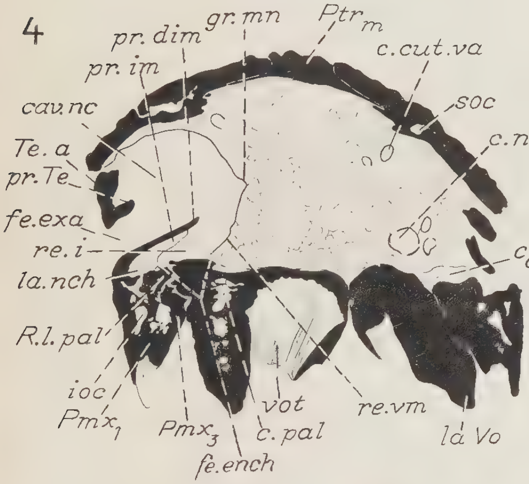
4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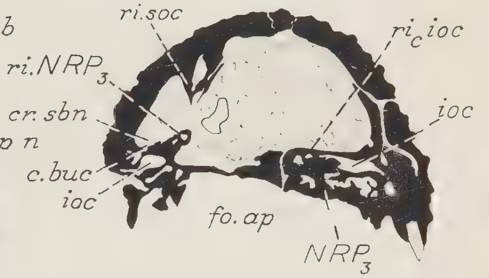
1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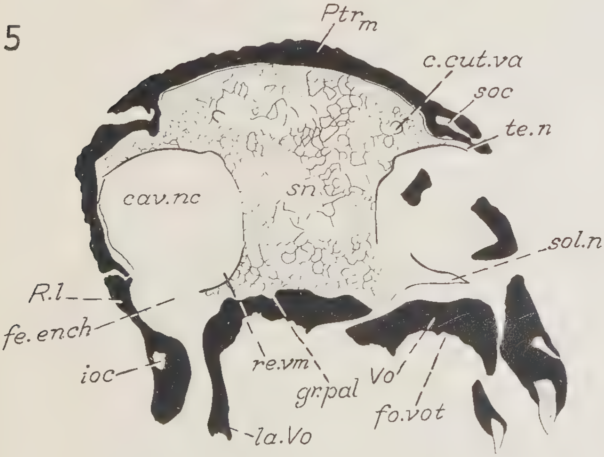
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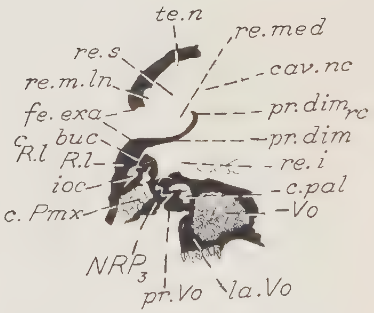
6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R.l
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re. i
ioc
c.pal
c. Pmx
Vo
NRP$_3$
pr.Vo
la.Vo

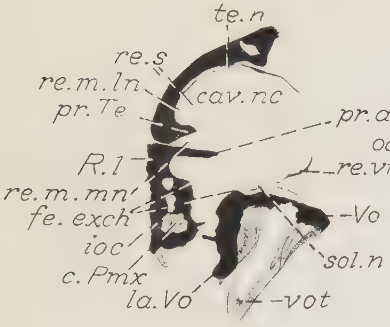
Plate 12.

Eusthenopteron foordi Whiteaves.

Six transverse sections through the snout. The sections are through the posterior part of the nasal cavity and through the postnasal wall. 5/2. Figs. 1—6. Sections Nos. 26, 29, 40, 50, 53 and 54 of grinding-series 2.

Aup, pars autopalatina of palatoquadrate; *Dpl,* dermopalatine; *La,* lachrymal; *Mx,* maxillary; *Psph,* parasphenoid; Ptr_m, posterior median postrostral; *R.l.* lateral rostral: *Vo,* vomer; art_1m, medial autopalatine articular area; art_2m, medial ethmoidal articular area; *cart,* superficial part of endocranium probably formed of cartilage; *cav.nc,* nasal cavity; *c.cut.va,* canal for cutaneous vessel; *c.ln, c.mn,* canals for r. lateralis and r. medialis narium of n. profundus; *c.Mx, c.Pmx,* canals for nerves to maxillary and premaxillary teeth; *c.olf,* canalis olfactorius; *c.pr,* profundus canal; *cr.vm,* ventro-medial crest of pars autopalatina; $c_1cut.va$, first branch of canal for cutaneous vessel; *fe.ench,* fenestra endochoanalis; *fe.exch,* fenestra exochoanalis; *fo.cr.vm,* pit receiving ventro-medial crest of pars autopalatina; *fo. vot,* pit of missing vomerine tusk; *gr.soc,* groove for supraorbital sensory canal ridge; *ioc,* infraorbital sensory canal; *la.Dpl,* lateral tooth-bearing lamina of dermopalatine; *la.Vo,* vertical tooth-bearing lamina of vomer; $od.La + Mx$, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *pr.dim,* processus dermintermedius of lateral rostral; *pr.Te,* medial process of anterior tectal extending into nasal cavity; *re.m.ln,* recess for m. lateralis narium; *re.m.mn,* recess for m. medialis narium; *re.s,* recessus superior of nasal cavity; *re.vm,* ventro-medial recess of nasal cavity; *ri.Psph,* ventral tooth-bearing ridge of parasphenoid; *ri.soc,* supraorbital sensory canal ridge; *sh.Vo,* vomerine shelf; *s.olf,* median septum separating olfactory canals; *soc,* supraorbital sensory canal; *sol.n,* solum nasi; *te.n,* tectum nasi; *vot,* vomerine tusk; *w.lic,* ventral medially curved part of lateral nasal wall; *w.pn,* postnasal wall.

1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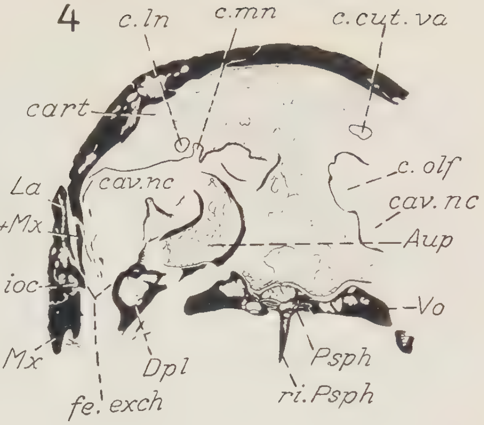
re.m.ln
pr.Te
cav.nc
pr.dim
R.l
re.vm
re.m.mn
fe. exch
Vo
ioc
sol.n
c. Pmx
la.Vo
vot

4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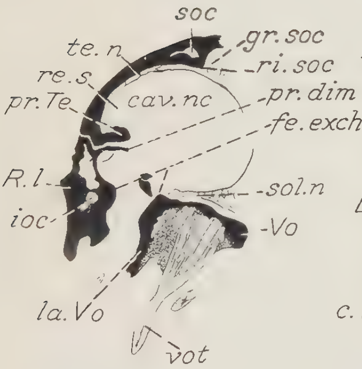
c.mn
c.cut.va
cart
c. olf
La
cav.nc
cav. nc
od.La+Mx
Aup
ioc
Vo
Mx
Dpl
Psph
fe. exch
ri.Psph

2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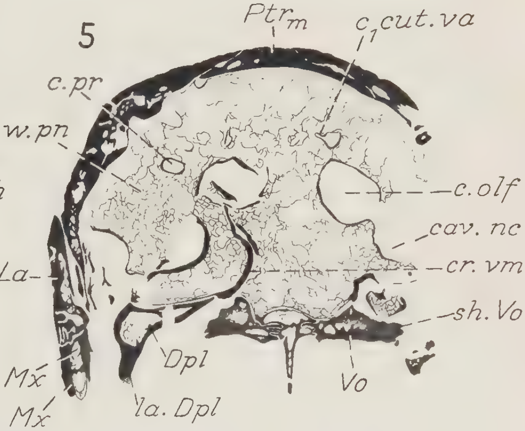
R.l
sol.n
ioc
Vo
la.Vo
vot

5


Ptr$_m$
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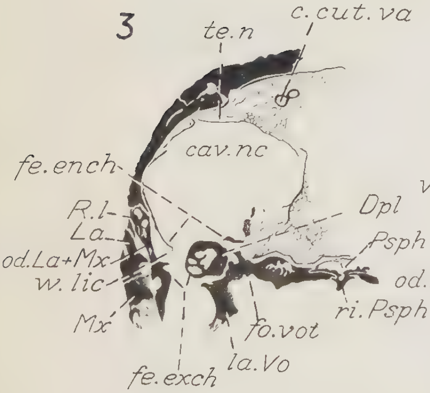
w.pn
c.olf
cav. nc
La
cr. vm
sh.Vo
Dpl
c. Mx
Vo
Mx
la. Dpl

3


te.n
c. cut. va
cav.nc
fe.ench
R.l
Dpl
La
od.La+Mx
Psph
w. lic
Mx
ri. Psph
fo.vot
fe.exch
la.Vo

6

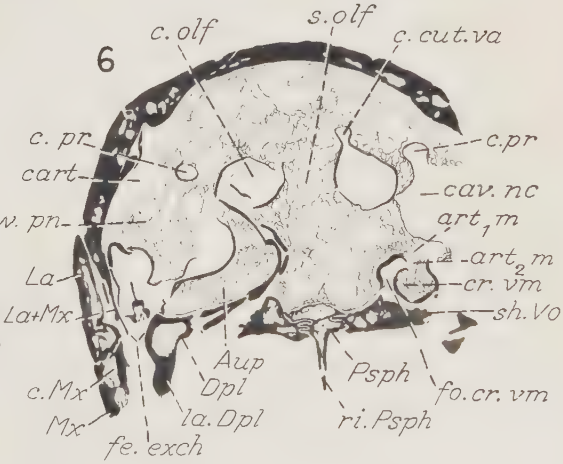

c. olf
s.olf
c. cut.va
c. pr
c.pr
cart
cav. nc
w. pn
art$_1$m
La
art$_2$m
cr. vm
od.La+Mx
sh.Vo
Aup
Dpl
Psph
fo.cr. vm
c.Mx
la. Dpl
ri.Psph
Mx
fe. exch

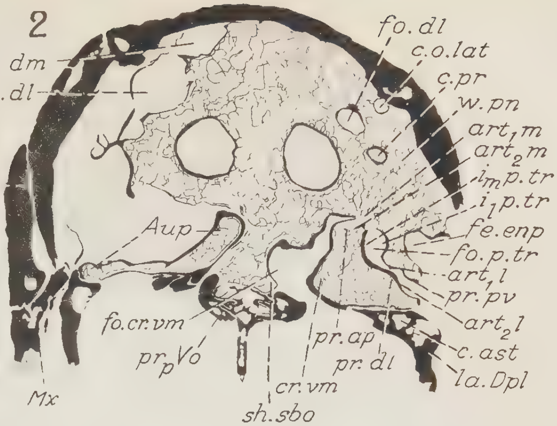
Plate 13.

Eusthenopteron foordi Whiteaves.

Five transverse sections through the snout. The sections are through the postnasal wall and the anterior part of the interorbital wall. Figs. 1—5. Sections Nos. 57, 62, 66, 76 and 87 of grinding-series 2. 5/2.

Aup, pars autopalatina of palatoquadrate; *Dpl*, dermopalatine; *Enpt*, entopterygoid; *La*, lachrymal; *Mx*, maxillary; *Psph*, parasphenoid; *Scl.pl*, sclerotic plates; art_1l, lateral autopalatine articular area; art_2l, lateral ethmoidal articular area; art_1m, medial autopalatine articular area; art_2m, medial ethmoidal articular area; *cart*, area of endocranium probably slightly ossified or cartilaginous; *c.ast*, canal for postchoanal nerve anastomosis; *c.ca*, canal for v. cerebralis anterior; *c.cut.va*, canal for cutaneous vessel; $c_{La_2}buc$, canal for branch of r. buccalis lateralis supplying sensory canal organ in lachrymal; *c.Mx*, canal in maxillary for nerve to maxillary teeth; *c.o.lat*, canal for r. ophthalmicus lateralis; *c.olf*, canalis olfactorius; *c.pr*, profundus canal; *cr.susp*, crista suspendens; *cr.vm*, ventro-medial crest of pars autopalatina; $c_7o.lat$, canal for branch of r. ophthalmicus lateralis to canal organ in nasal 7; *dplt*, dermopalatine tusk; *f.buc*, foramen for r. buccalis lateralis; *fe.enp*, fenestra endonarina posterior; *fe.o*, orbital opening; *fo.cr.vm*, pit receiving ventro-medial crest of pars autopalatina; *fo.dl*, *fo.dm*, dorso-lateral and dorso-medial depressions on posterior face of postnasal wall; *fo.p.tr*, pit for insertion of portio transversalis of m. levator bulbi; *gr.lev*, groove for origin of principal portion of m. levator bulbi; *gr.ntp*, groove, probably for posterior nasal tube; $i_{lp}.tr$, notch forming lateral wall of pit for insertion of portio transversalis of m. levator bulbi; $i_{mp}.tr$, notch forming medial wall of pit for insertion of portio transversalis of m. levator bulbi; *ioc*, infraorbital sensory canal; *la.Dpl*, lateral vertical tooth-bearing lamina of dermopalatine; *la.so*, lamina supraorbitalis; *od.La + Mx*, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *pr.ap*, processus apicalis of pars autopalatina; *pr.dl*, dorso-lateral process of pars autopalatina; *pr.Mx*, antero-dorsal medially curved process of maxillary; *pr.pv*, postero-ventral process of ethmoidal region; pr_pVo, posterior process of vomer; *pr.sol*, processus supraorbitalis lateralis; *ri.dl*, *ri.dm*, dorso-lateral and dorso-medial ridges on posterior face of postnasal wall; *ri.olf*, olfactory ridge; *ri.Psph*, ventral tooth-bearing ridge of parasphenoid; *ri.soc*, supraorbital sensory canal ridge; s_dio, thin dorsal part of interorbital wall; *sh.sbo*, anterior suborbital ledge; *soc*, supraorbital sensory canal; *s.olf*, median septum separating olfactory canals; s_vio, thin ventral part of interorbital wall; *w.pn*, postnasal wall.

2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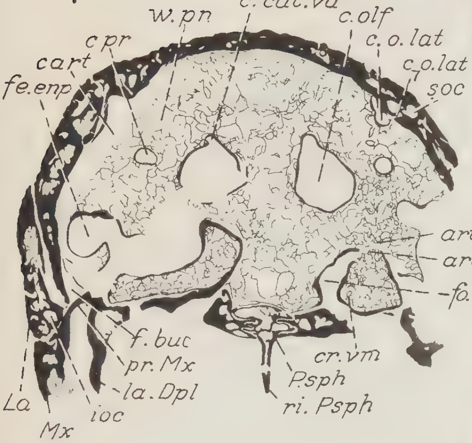
fo.dl
c.o.lat
c.pr
w.pn
art$_1$m
art$_2$m
i$_m$p.tr
i$_1$p.tr
fe.enp
fo.p.tr
art$_1$l
pr.pv
art$_2$l
c.ast
la.Dpl
pr.dl
pr.ap
cr.vm
sh.sbo
pr$_p$Vo
fo.cr.vm
Aup
od.La+Mx
Mx

1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c.pr
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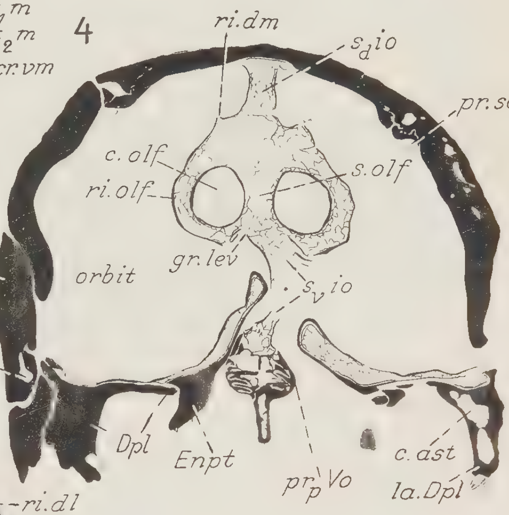
fe.enp
c.o.lat
c$_1$.o.lat
soc
art$_1$m
art$_2$m
fo.cr.vm
cr.vm
P.sph
ri.Psph
f.buc
pr.Mx
la.Dpl
La
Mx
ioc

4


ri.dm
s$_d$io
pr.sol
c.olf
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s.olf
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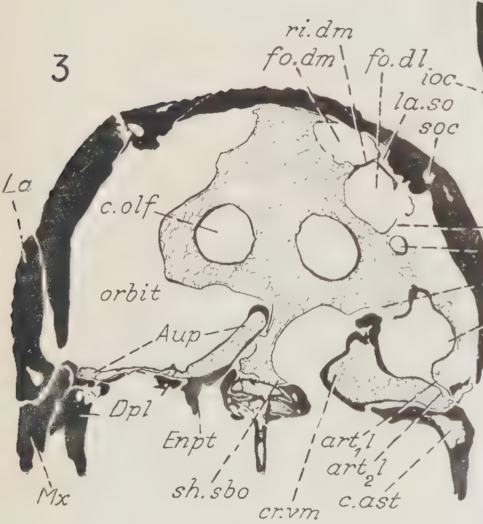
La
orbit
s$_v$io
ioc
Dpl
Enpt
pr$_p$Vo
c.ast
la.Dpl

3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fo.dm
fo.dl
la.so
soc
La
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ri.dl
c.pr
art$_1$m
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Dpl
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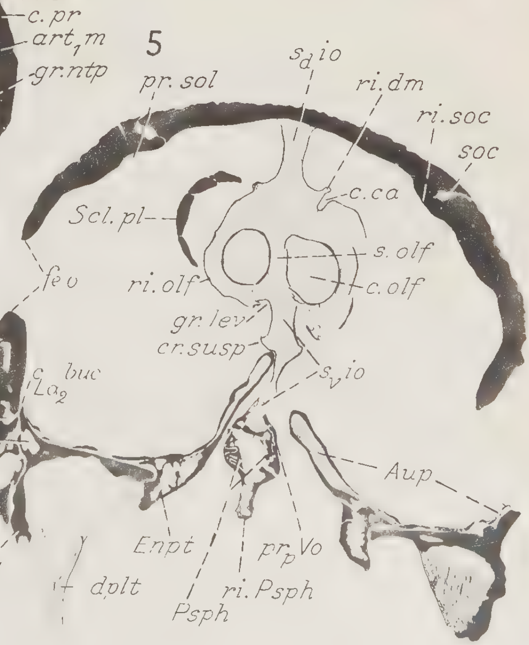
art$_2$l
c.ast

5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soc
c.ca
Scl.pl
s.olf
ri.olf
c.olf
fe.o
gr.lev
cr.susp
s$_v$io
La
c buc
La$_2$
ioc
c. ast
c. Mx
Aup
Enpt
pr$_p$Vo
ri. Psph
Psph
la. Dpl
dolt

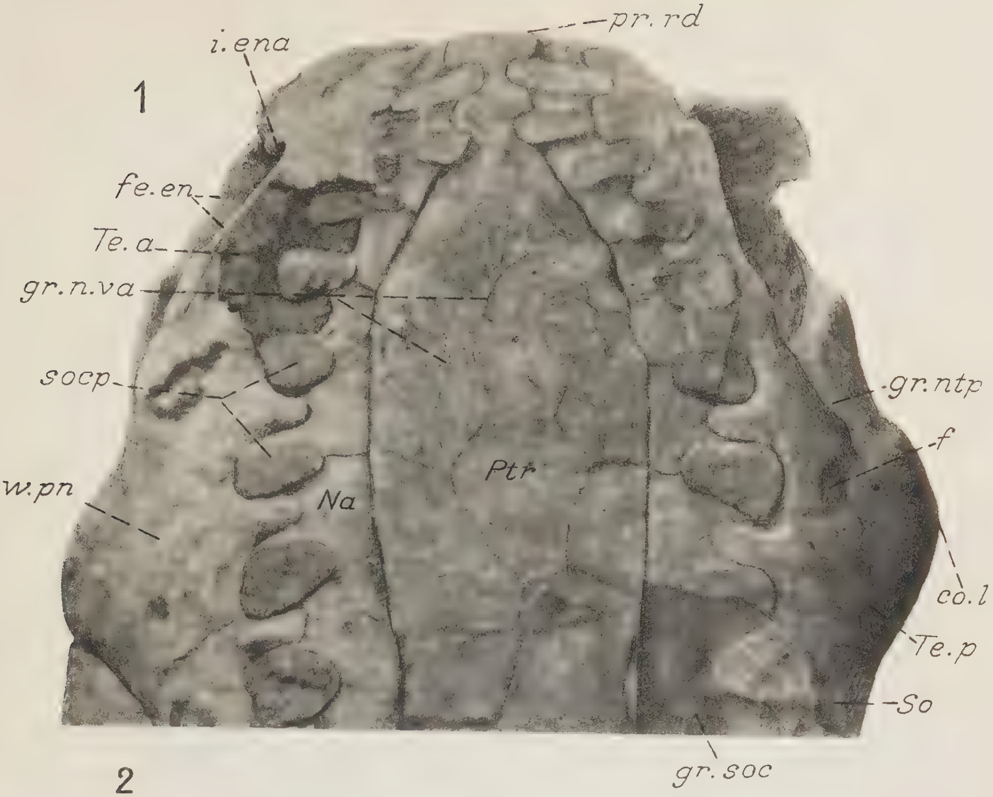
Plate 14.

Euporosteus eifelianus Jaekel.

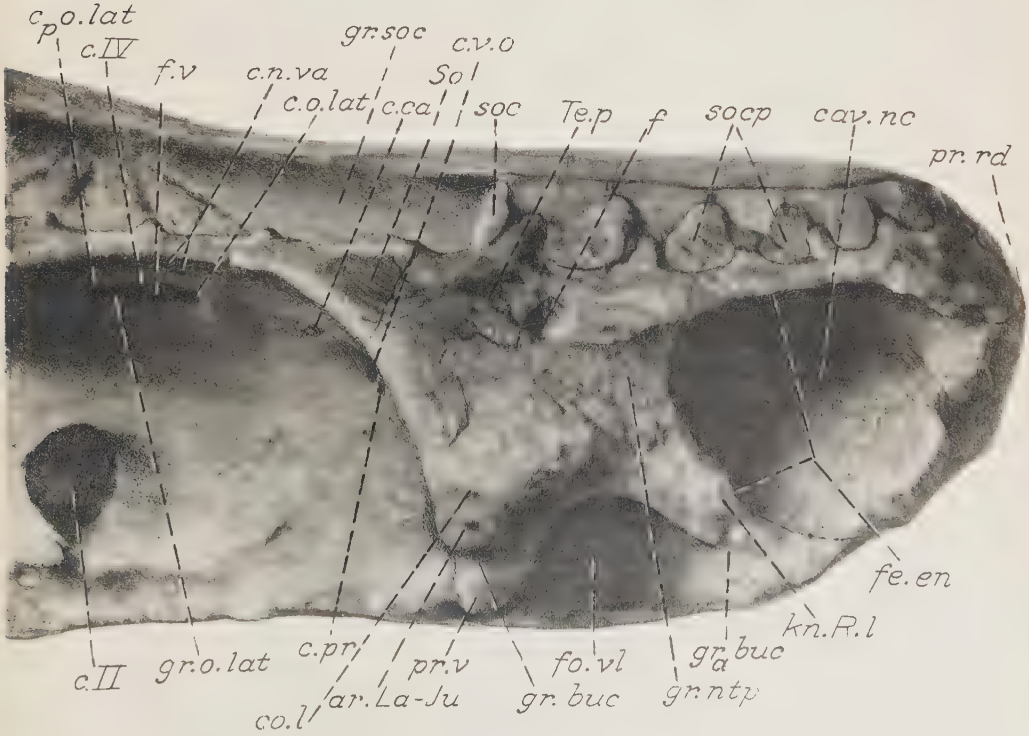
Snout of the holotype. The dermal bones almost entirely weathered away. From the Upper Devonian? of Gerolstein. Geological-Palaeontological Institute, University of Berlin. 9/1. Fig. 1 in dorsal view, and fig. 2 from the right side. Figured by JAEKEL (1927, figs. 23, 49) and STENSIÖ (1937 a, figs. 9, 10; pl. 11, figs. 3, 4; pl. 12).

Na, impression of nasal; *Ptr*, impression of postrostral; *So*, supraorbital; *Te.a*, anterior tectal; *Te.p*, posterior tectal; *ar.La-Ju*, area for attachment of anterior end of the lachrymojugal; *cav.nc*, nasal cavity; *c.ca*, canal, probably for v. ophthalmica; *c.n.va*, canals for twigs of nerves and vessels; *co.l*, lateral corner of ethmoidal region; *c.o.lat*, *c*$_{p}$*o.lat*, anterior and posterior canals for r. ophthalmicus lateralis; *c.pr*, anterior profundus canal; *c.v.o*, canal, probably for a. ophthalmica; *c.II*, *c.IV*, canals for n. opticus and trochlearis; *f*, indistinct foramen; *fe.en*, fenestra endonarina communis; *fo.vl*, fossa ventro-lateralis of postnasal wall; *f.v*, vein foramen; *gr*$_{a}$*buc*, *gr.buc*, anterior and posterior grooves for r. buccalis lateralis; *gr.ntp*, groove for the thickened anterior part of the posterior tectal, pierced by canal for posterior nasal tube; *gr.n.va*, grooves for twigs of nerves and vessels; *gr.o.lat*, groove for r. ophthalmicus lateralis; *gr.soc*, groove for supraorbital sensory canal ridge; *i.ena*, notch for anterior nasal tube; *kn.R.l*, protuberance for attachment of lateral rostral; *pr.rd*, dorsal rostral process; *pr.v*, ventral process of postnasal wall; *soc*, *socp*, supraorbital sensory canal and pores; *w.pn*, postnasal wall.

1


pr.rd
i.ena
fe.en
Te.a
gr.n.va
socp
w.pn
Na
Ptr
gr.ntp
f
co.l
Te.p
So
gr.soc

2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f.v
c.n.va
c.o.lat
gr.soc
c.ca
c.v.o
So
soc
Te.p
f
socp
cav.nc
pr.rd
fe.en
kn.R.l
gra buc
c.II
gr.o.lat
c.pr
pr.v
ar.La-Ju
co.l
gr.buc
fo.vl
gr.ntp

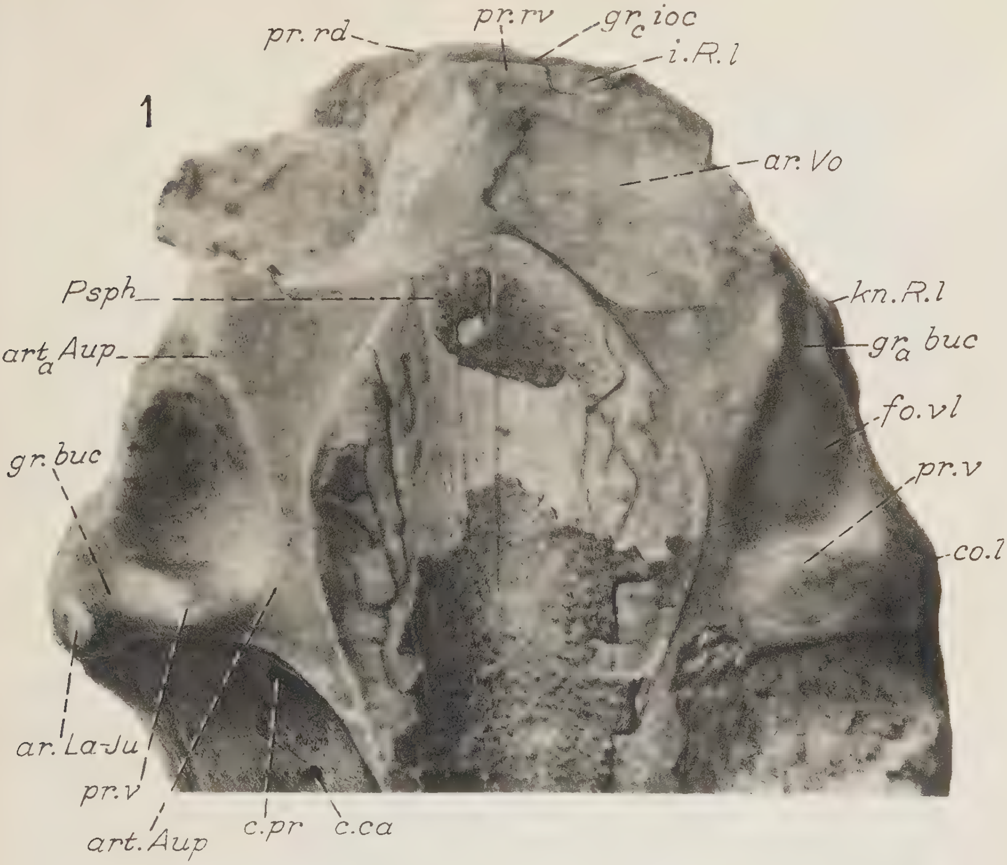
Plate 15.

Euporosteus eifelianus Jaekel.

The same snout as shown in pl. 14. 9/1. Fig. 1 in ventral view, and fig. 2 from the left side.

Na, impression of nasal; *R.l*, lateral rostral; *Te.a*, anterior tectal; *Te.a?*, fragment of dermal bone, probably of the most anterior of the anterior tectals; *Psph*, parasphenoid; *ar.La-Ju*, area for attachment of anterior end of lachrymo-jugal; *ar.R.l*, area for attachment of lateral rostral; *ar.Vo*, vomeral area; *art.Aup*, autopalatine articular area; *art*$_a$*Aup*, autopalatine articular facet; *c.ca*, canal, probably for v. ophthalmica; *co.l*, lateral corner of ethmoidal region; *c.pr*, profundus canal; *fe.en*, fenestra endonarina communis; *fo.vl*, ventro-lateral fossa of postnasal wall; *gr*$_a$*buc*, *gr.buc*, anterior and posterior grooves for r. buccalis lateralis; *gr*$_c$*ioc*, groove for the rostral elements lodging ethmoidal commissure of infraorbital sensory canals; *gr.ntp*, groove for the thickened anterior part of the posterior tectal, pierced by canal for posterior nasal tube; *i.ena*, notch for anterior nasal tube; *ioc*, infraorbital sensory canal; *i.R.l*, notch for antero-ventral end of lateral rostral; *kn.R.l*, protuberance for attachment of lateral rostral; *pr.rd*, *pr.rv*, dosal and ventral rostral processes; *pr.v*, ventral process of postnasal wall; *socp*, pore of supraorbital sensory canal.

1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gr_c ioc
i.R.l
ar. Vo
Psph
kn.R.l
art_a Aup
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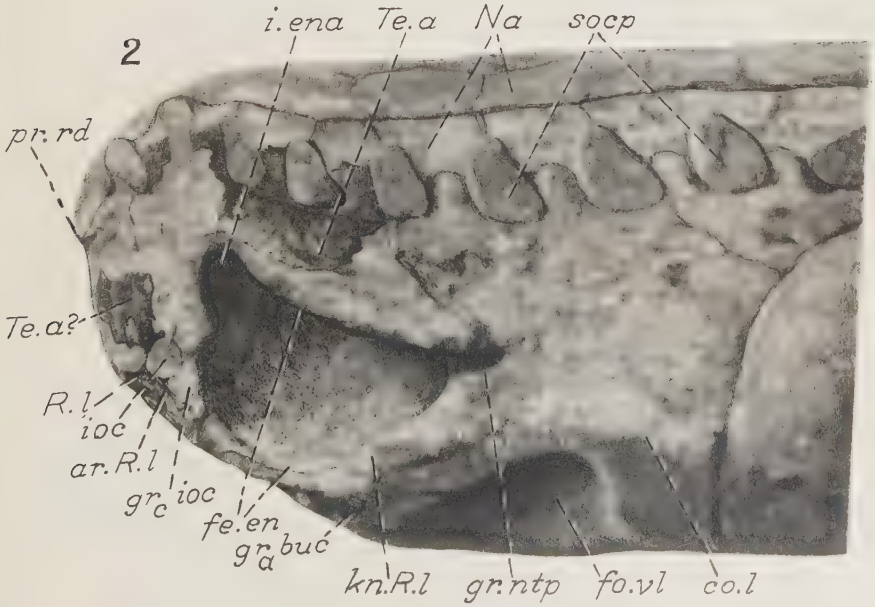
pr.v
co.l
ar. La-Ju
pr.v
art. Aup
c.pr
c.ca

2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Te.a
Na
socp
pr. rd
Te.a?
R.l
ioc
ar. R.l
gr_c ioc
fe.en
gr_a buc
kn.R.l
gr.ntp
fo.vl
co.l

Plate 16.

Fig. 1. *Euporosteus eifelianus* Jaekel. Holotype. Same specimen as in pls. 14 and 15. Postnasal wall of right side seen from behind. 9/1.

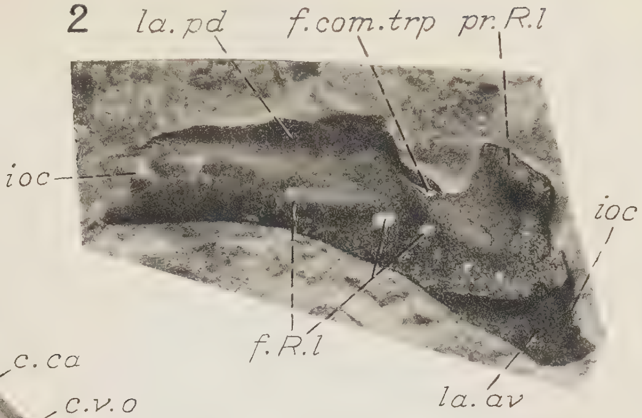
Fig. 2. *Diplocercides kayseri* (v. Koenen). Holotype. Lateral rostral of left side in medial view. Figured by Stensiö (1937 a, pl. 10, fig. 1) but later on further prepared. Geological-Palaeontological Institute of the University of Göttingen. 12/1.

Fig. 3. *Diplocercides kayseri* (v. Koenen). Cast of a lower part of the right nasal cavity in ventral view. Specimen *a* of Stensiö's description in 1937 (1937 a, pl. 2). Geological-Palaeontological Institute of the University of Berlin. 10/1.

Fig. 4. *Nesides schmidti* Stensiö. Holotype. Right posterior tectal in medial view. The specimen was figured by Stensiö (1937 a, pl. 10, figs. 2 and 3) but has later on been further cleaned. Geological-Palaeontological Institute of the University of Göttingen. 10/1.

So, supraorbital; *Te.p*, posterior tectal; *ar.La-Ju*, area for attachment of anterior end of lachrymo-jugal; *c.a.on*, canal, probably for an orbitonasal artery; *cav.nc*, nasal cavity; *c.ca*, canal, probably for v. ophthalmica; *c.olf*, canalis olfactorius; *c.ntp*, canal in posterior tectal for posterior nasal tube; *c.pr*, anterior profundus canal; *c.v.o*, canal, probably for a. ophthalmica; *f.com.trp*, foramen for large ascending tube of infraorbital sensory canal (this tube corresponds to the posterior transverse commissural sensory canal in Coelacanthids of later geological periods); *f.R.l*, canals for branches of r. buccalis lateralis, r. maxillaris V and vessels; fe_1exp, fe_2exp, fenestrae exonarinae posteriores; *gr.buc*, posterior groove for r. buccalis lateralis; *ioc*, infraorbital sensory canal; *la.av*, *la.pd*, antero-ventral and postero-dorsal facial laminae of lateral rostral; my_v, ventral anterior myodome; *om*, margin of orbital opening; *pr.aot*, antotic process of ethmosphenoid; *pr.R.l*, antero-dorsal process of lateral rostral; *pr.v*, ventral process of postnasal wall; *re.am*, antero-medial recess of nasal cavity.

2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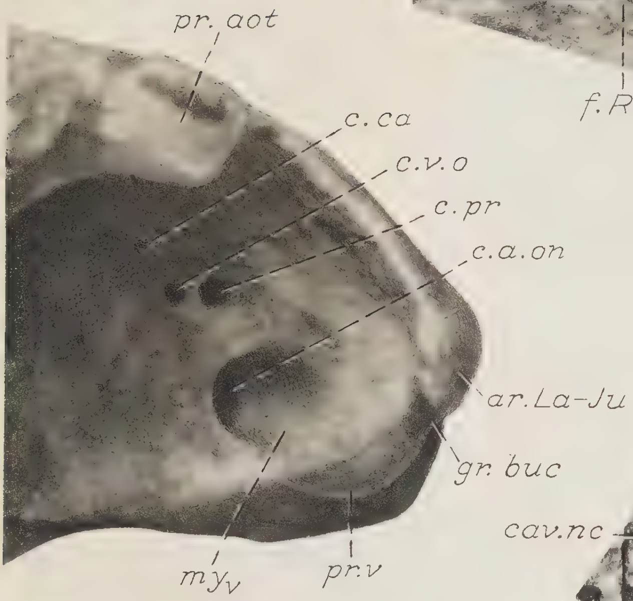
ioc
ioc
f.R.l
la.av

1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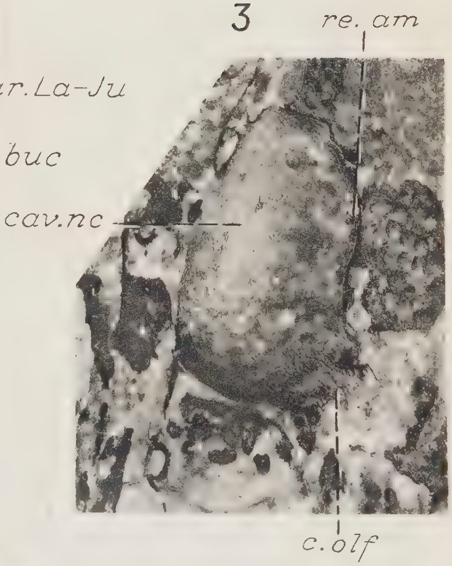
ar.La-Ju
gr.buc
my_v
pr.v

3


re.am
cav.nc
c.olf

4

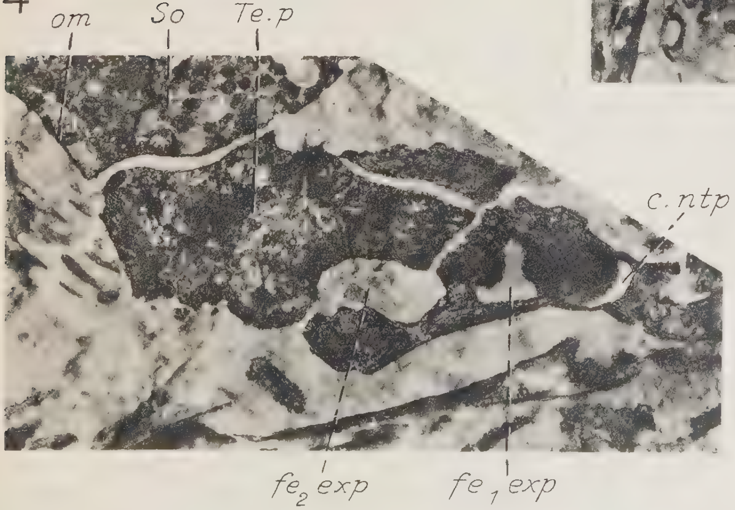

om
So
Te.p
c.ntp
fe_2 exp
fe_1 exp

Plate 17.

Dictyonosteus arcticus Stensiö.

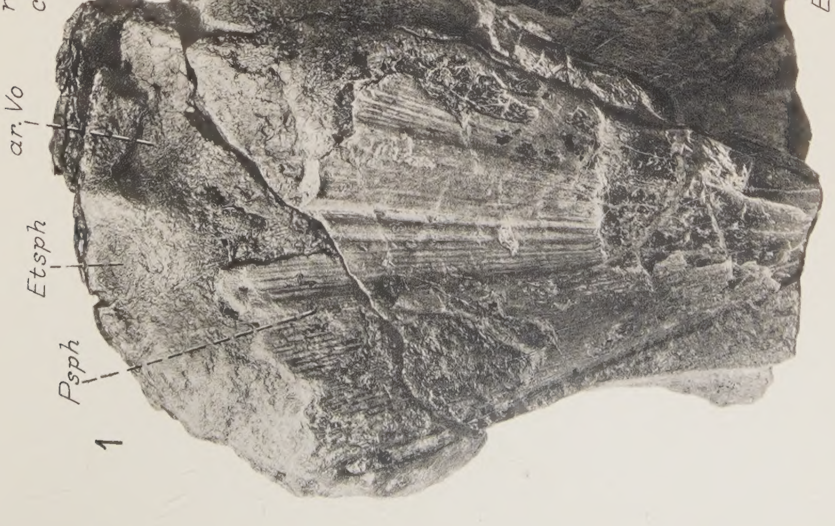
Holotype. Anterior deficient part of the divisio cranialis anterior. The specimen has been figured several times by STENSIÖ (1918, pls. 4—6; 1922 a, pl. 1, figs. 1—4; 1925, fig. 13) but has recently been further prepared. Palaeontological Institute of the University of Uppsala.

Figs. 1 and 2. The anterior part of the divisio cranialis anterior in lateral and ventral views. 5/4.

Fig. 3. The same part of the divisio cranialis anterior as in figs. 1 and 2 but with a lateral part removed in order to show the medial part of the left nasal cavity. Lateral view. 5/3.

Fig. 4. The part removed in fig. 3 in medial view. We see here the lateral part of the nasal cavity. 5/3.

Etsph, ethmosphenoid; *Psph*, parasphenoid; *Te.a*, anterior tectal; *ar.Vo*, vomeral area; *c.a.on*, canal, probably for orbitonasal artery; *cav.nc*, nasal cavity; *cav.rm*, cavity, probably corresponding to the median rostral cavity in *Latimeria*; *c.ca*, canal for v. cerebralis anterior; *c.o.lat*, anterior canal for r. ophthalmicus lateralis; *c.olf*, canalis olfactorius; *c.ond*, canal, probably for a branch of the orbitonasal artery; *c.pr?*, canal, possibly for n. profundus; *c.te*, canal piercing tectum nasi; *c.v*, canal, probably for a branch of v. cerebralis anterior; *fe.en*, fenestra endonarina communis; *fo.vl*, fossa ventro-lateralis of postnasal wall; my_d + *o.lat*, compressed pit, probably corresponding to the posterior widened part of the canal *c.o.lat* in *Nesides*; my_v, ventral anterior myodome; *re.am*, antero-medial recess of nasal cavity; *te.o*, tectum orbitale; $te_x o$, fracture of tectum orbitale; *w.m*, wall between nasal cavity and median rostral cavity; *w.pn*, postnasal wall.


1
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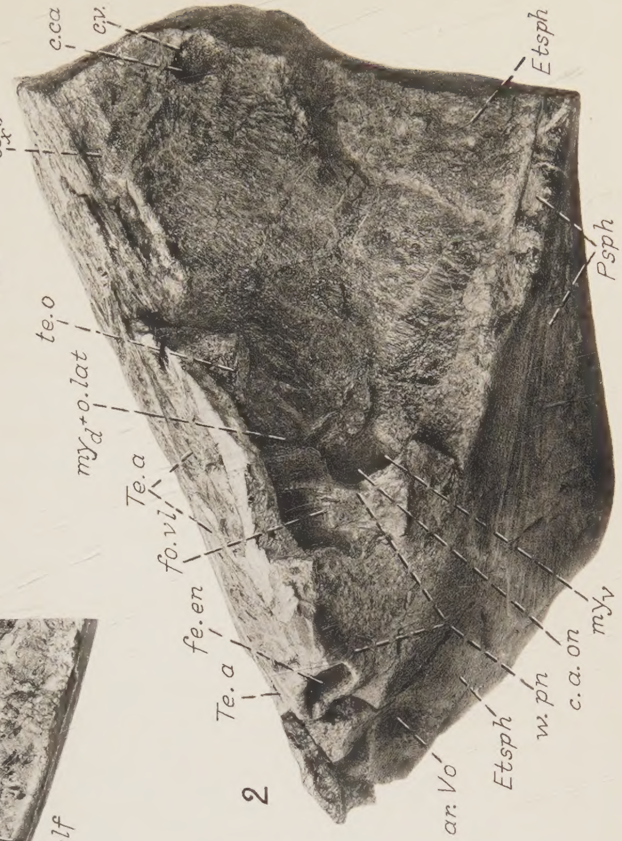
Psph
fe.en
w.pn
fo.vl
te.o
Etsph


2
c.ca
c.v.
te$_x$o
Etsph
Psph
te.o
my$_d$+o.lat
Te.a
fo.vl
fe.en
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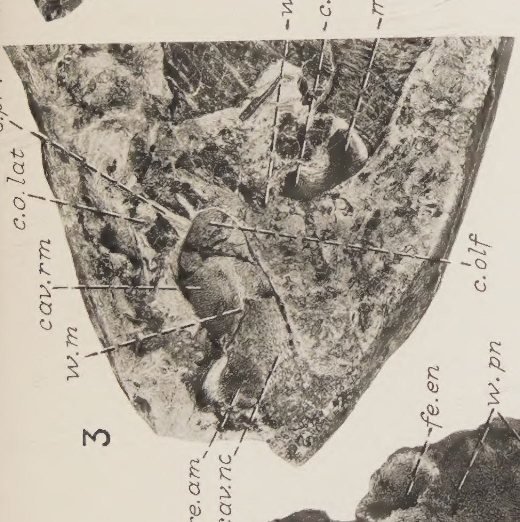
Etsph
w.pn
c.a.on
my$_v$


3
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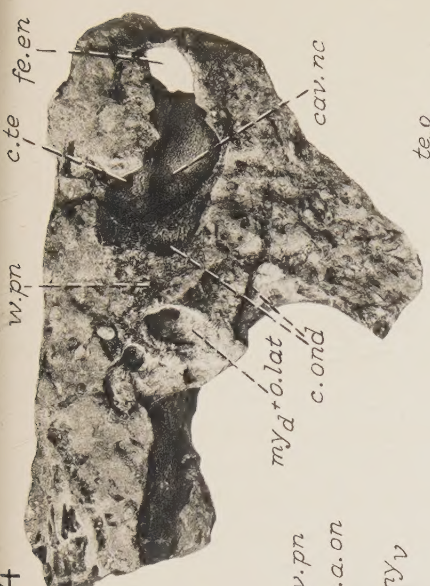
4
fe.en
c.te
cav.nc
w.pn
my$_d$+o.lat
c.ond